

**PROGRESS IN THE
PHYSIOLOGY OF FARM ANIMALS**

Progress in the
PHYSIOLOGY
OF
FARM ANIMALS

Edited by
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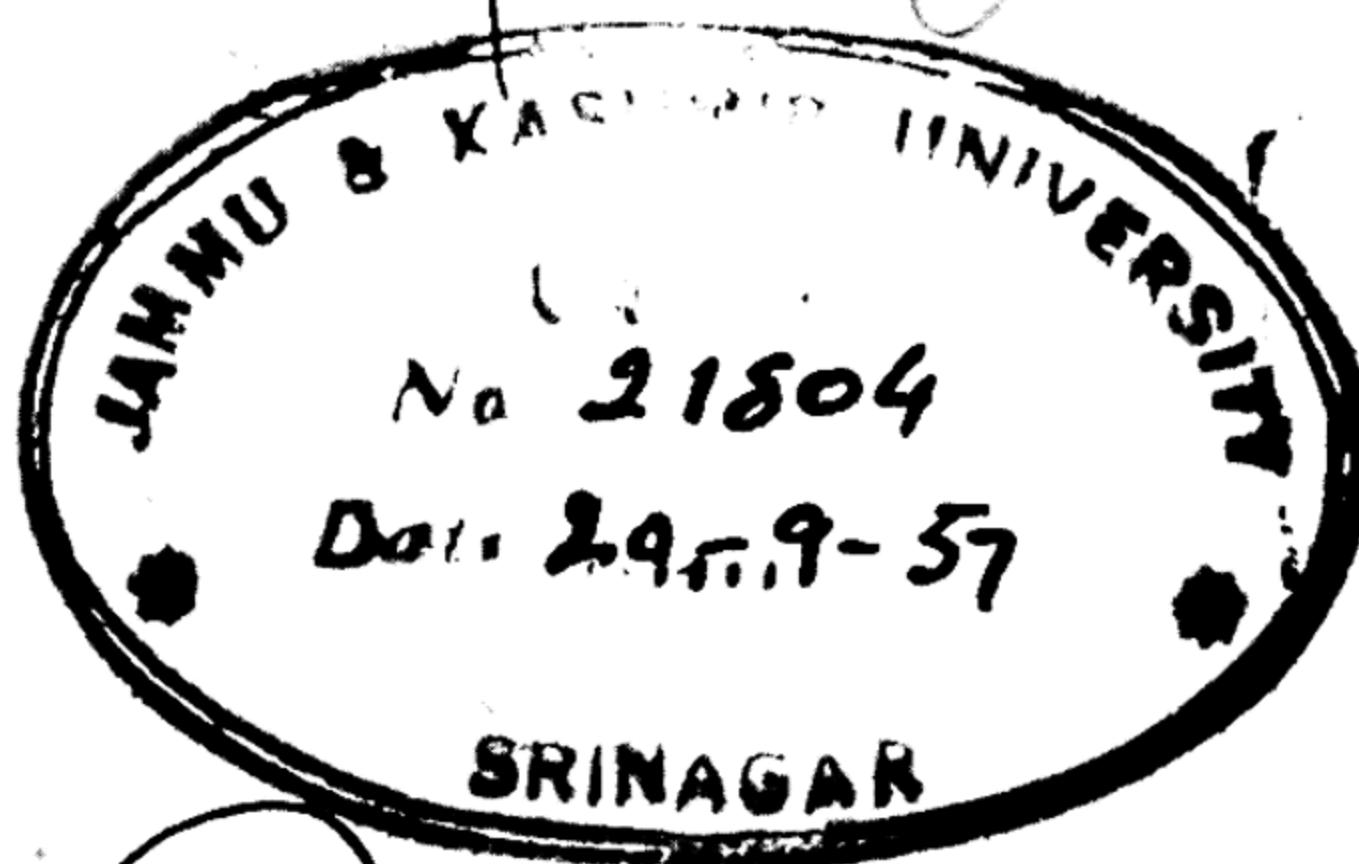
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GROWTH

CHAPTER 9

LIVE-WEIGHT GROWTH

BY R. W. POMEROY

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THE phenomenon of growth is one of the most important processes in practical agriculture; in fact it would be true to say that almost the whole of agricultural production is based fundamentally on some aspect of the growth process. Indeed, the importance of growth is by no means limited to agriculture and the study of growth has widespread applications throughout the biological sciences and in medicine. For example, studies of the heights and weights of children at different ages and under various nutritional régimes have led to great improvements in child nutrition and welfare.

It is not surprising, therefore, that growth which seems at first to be quite a simple process should, on analysis, prove to be very complex. A definition of what growth really is must obviously be a necessary preliminary to a quantitative study of growth, but defining growth has not proved to be an easy matter. For example SCHLOSS (1911) defined growth as 'correlated increase in mass of the body in definite intervals of time in a way characteristic of the species'. This definition recognizes the fact that growth in weight of an organism is ultimately a function of the heredity of the species subject to individual variability. It does not, however, cover the fact that animals kept on a maintenance or even a submaintenance diet may increase in size because their bones continue to grow while the weight of the body remains constant or even diminishes.

BRODY (1945) defined growth as 'a relatively irreversible time-change in the measured dimension'. This definition covers growth in size as well as in weight and the concept of irreversibility implicitly excludes fluctuations due to variations in food supply and to gestation and lactation. According to this definition an animal kept at constant weight does not grow in respect of the measured dimension of body weight but it does grow in respect of the measured dimension of length of bone. The exclusion of random short-term fluctuations in body weight appears more reasonable than does the exclusion of long-term decreases in weight resulting from a submaintenance diet or the strain of lactation which are a form of negative growth even though

the composition of the weight loss may be different from the composition of the weight gain over the same weight range.

MAYNARD (1947) distinguishes between 'true growth' and the deposition of fat in the adipose tissues. He regards true growth as an increase in the weight of the organs and of the structural tissues such as muscle and bone. On this basis growth is characterized primarily by an increase in protein, minerals and water. However, while it is sometimes convenient, agriculturally, to distinguish between 'growth' and 'fattening' the distinction is an arbitrary one and there seems to be no logical reason for regarding the deposition of fat in the fat depots as not being part of the growth process. The exclusion of fat, presumably on the ground that it constitutes a nutrient reserve, implies that it is possible to differentiate between fat which has a functional significance and fat which is simply reserve food material. This is difficult to substantiate in practice since, for example, the inner layer of subcutaneous fat in the pig undoubtedly constitutes a reserve of food material but at the same time, through its insulating properties, it has a functional significance in thermo-regulation. Furthermore if deposition of fat is excluded from growth it would seem equally logical to exclude some of the water which is taken from the environment and incorporated unchanged into the tissues.

GROWTH CURVES

The curve of growth produced by plotting weight against age is sigmoid, *i.e.* roughly S-shaped and is much the same shape for all species except that in the case of man the juvenile period is exceptionally long. In most of the higher animals puberty occurs after about 30 per cent of the mature weight has been achieved whereas in man it does not occur until about 60 or 70 per cent of the mature weight has been achieved (*Figure 9.1*, from Brody, 1945).

The general shape of the growth curve is produced by the interaction of two opposing forces, a growth accelerating force and a growth retarding force. When the slope of the growth curve is increasing, the growth accelerating force is predominating and when the slope of the growth curve is diminishing, the growth retarding force is predominating. The growth accelerating force arises from the nature of growth in weight which is a summation of cell multiplication, cell hypertrophy and the inclusion of material taken from environment. In the absence of inhibiting factors living cells are capable of growing for an indefinite period as was shown by LOEB (1908) for the cells of cancer tissue and later by CARRELL (1933) for the cells of normal tissue. The individual cells tend to reproduce at a constant rate so that the growth of the mass of cells representing the whole organism

LIVE-WEIGHT GROWTH

tends to be self-accelerating. For this reason the part of the growth curve during which the growth accelerating force is dominant is sometimes referred to as the 'self-accelerating phase of growth'.

Within the closed system represented by the animal body there comes a stage in growth when further growth tends to be limited by growth inhibiting factors such as availability of nutrients and lack

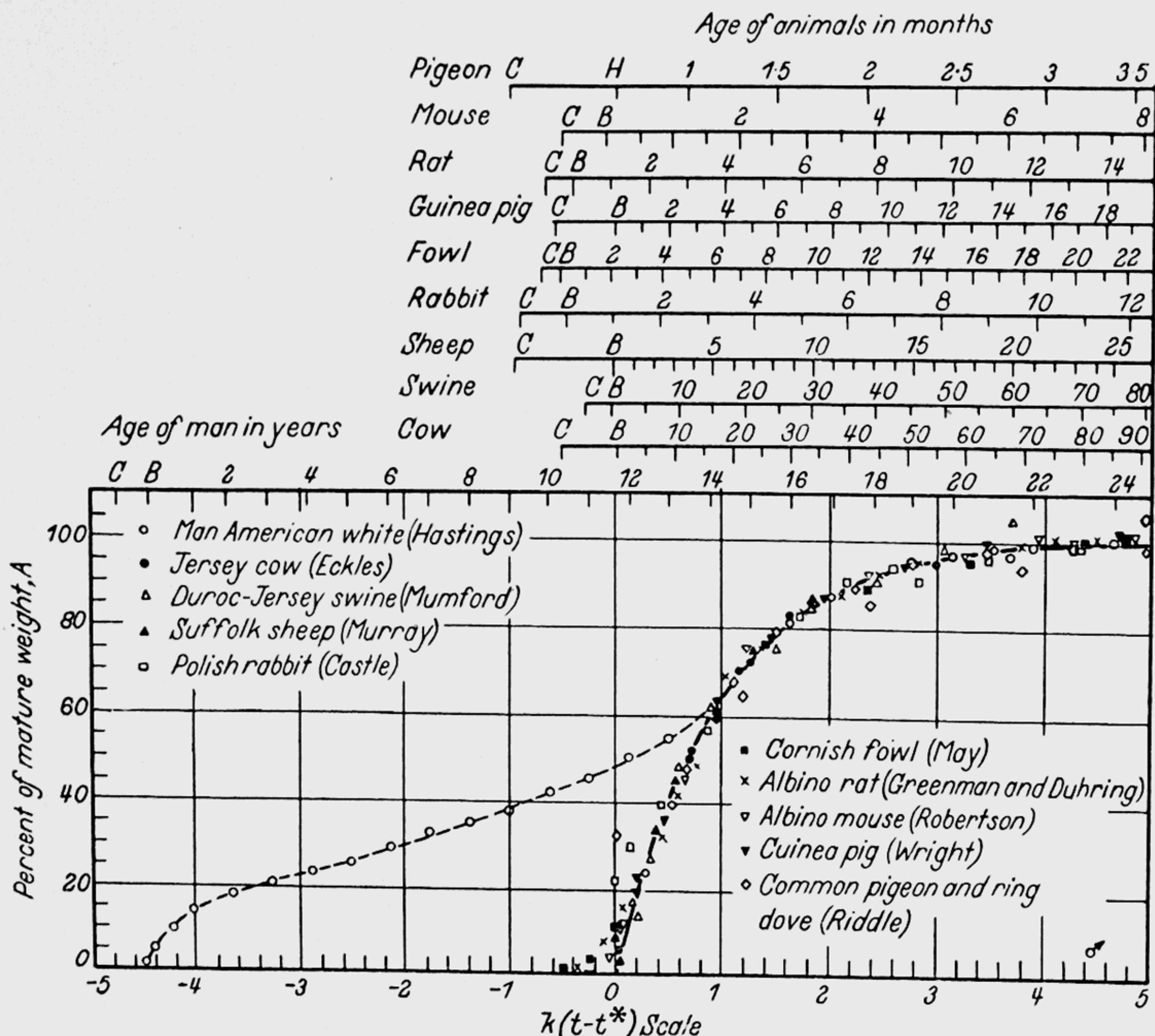


Figure 9.1. 'Weight growth equivalents of farm animals, laboratory animals and man.' (From Brody (1945), by courtesy Reinhold.)

of space. From this point growth is limited by the growth retarding force and this part of the growth curve is consequently referred to as the 'self-retarding phase of growth'. Ultimately growth is completely inhibited by the environment and this is followed by senescence and finally by death.

Where the two segments of the growth curve represented by the self-accelerating and self-retarding phases of growth intersect is a point of inflection. This point of inflection represents the point in the growth curve when the acceleration of growth has ended and the retardation of growth is about to begin, and it is therefore the point at which growth rate is at a maximum. This inflection which

occurs in the growth curve of all animals including man coincides with puberty and for that reason is often referred to as the pubertal inflection.

MEASURES OF GROWTH

The commonest measure of growth is probably increase in live weight but frequently various measures of size such as height and length are also used. A combination of live weight and measures of size is frequently more informative than live weight alone because it records the changes in shape which occur during normal growth and also demonstrates that an animal may continue to increase in size even though the body weight is kept constant.

Rate of growth in weight may be expressed as average growth rate, that is, as absolute gain in weight per unit time, *i.e.* it may be expressed by the formula $\frac{W_2 - W_1}{t_2 - t_1}$ where $W_2 - W_1$ is the gain in weight during the time interval $t_2 - t_1$. This average growth rate is frequently used in animal experiments when the results of the experiment are summarized by saying that, for example, during the experimental period treated animals gained x pounds per day whereas the control animals only gained y pounds per day. The average growth rate expressed in this way is open to no very great objection providing that the interval $t_2 - t_1$ is short. If $t_2 - t_1$ is long the average growth rate gives no idea of the growth rate at any particular time. Consideration of the shape of the typical growth curve indicates that the average growth rate calculated for the whole period from conception to maturity could be grossly misleading.

An alternative method of expressing growth rate is by means of the relative growth rate, that is, the weight gained in a given time expressed in relation to the weight at the beginning of that time.

Relative growth rate is therefore expressed by the formula $\frac{W_2 - W_1}{W_1}$

where W_1 is the initial weight and W_2 is the final weight. For convenience relative growth rate is usually expressed as a percentage and is useful for comparing growth in different species of widely different body weights. Again the formula for relative growth rate can be misleading if the gain in weight is very large in comparison with the initial weight. Under these conditions the relative growth rate gives no idea of the growth rate at the time when the final weight was recorded.

Brody (1945) has suggested that instead of the average growth rate $\frac{W_2 - W_1}{t_2 - t_1}$ the 'instantaneous growth rate' should be used. The

instantaneous growth rate is obtained by dividing the instantaneous

weight gain dW/dt by the weight W which is the weight at which dW/dt is measured.

$$\text{i.e. Instantaneous relative growth rate, } k = \frac{dW/dt}{W}$$

This is useless for practical purposes because of the impossibility of measuring the instantaneous weight gain dW/dt so the formula is written in the integrated form

$$\text{i.e. } W = A e^{kt}$$

where e is the base of natural logarithms and A is the natural logarithm of W when $t = 0$.

This formula is applicable to the self-accelerating phase of growth when the relative growth rate is a function of growth already made. During the self-inhibiting phase of the growth curve the relative growth rate is a function, not of growth already made, but of growth yet to be made to reach maturity

$$\text{i.e. } \frac{dW}{dt} = -k(A - W)$$

where A is the mature weight. The integrated form of this equation is

$$W = A - B e^{-kt}$$

where A is the mature weight and B is a constant.

These equations have been used by Brody for calculating equivalent growth rates for different species and for different breeds of the same species.

Other more elaborate equations have been proposed mostly involving the introduction of additional constants which have the effect of transforming the equation into a potential series. The introduction of a large number of constants into an equation increases its flexibility but tends to reduce its biological significance. The chief purpose of applying mathematical formulation to growth data is to facilitate the handling and interpretation of what is usually an unwieldy mass of observations. Consequently elaboration of mathematical treatment is only justifiable if it simplifies the interpretation of the observations, and any tendency towards mathematical elaboration without a corresponding gain in biological significance is best avoided.

Attempts to evolve mathematical laws of growth on the basis of so-called axioms relating to "growth metabolism" have, in recent years, incurred a good deal of criticism mainly on the ground that the so-called axioms on which the calculations are based are invalid. The mathematical approach to the study of growth has been discussed by Brody (1945) and MEDAWAR (1945).

It is implicit in the growth equation for growth following the pubertal inflection that individuals have an adult size which is

ultimately limited by their genetic constitution. This adult size cannot be exceeded but it may be reduced if environmental conditions are unfavourable. In the same way individuals tend to have characteristic relative growth rates but these may be modified by the action of various factors such as plane of nutrition, temperature, hormones, vitamins and trace elements.

Attempts have been made to construct 'normal' or standard growth curves, for example, for different breeds of cattle; but these standards need to be modified from time to time as more knowledge is gained of the factors which influence growth.

In general the rate at which an animal grows is of greater interest agriculturally than its mature weight. Few farm animals apart from draught horses and dairy cattle ever live long enough to reach their mature weight, but the rate at which they grow has a profound influence on their profitability particularly in the case of meat animals. This arises primarily from the fact that part of the food consumed by an animal during its lifetime is devoted merely to maintaining it, *i.e.* to keeping it alive and carrying out its vital functions such as digestion, respiration, circulation, thermo-regulation and locomotion. The proportion of the food devoted to its maintenance which is consumed by an animal is unprofitable from the point of view of the farmer, so that other things being equal, the lower the maintenance requirement of an animal, the greater will be its profitability at market weights. Although an animal which is under-fed may have a lower daily maintenance requirement than one which is well fed, the total maintenance requirement of the latter tends to be less because it reaches a marketable weight in a shorter period of time. However, it is becoming apparent that maximum growth rate at all ages may not always produce the best possible carcass conformation, so that the profit derived from reducing total maintenance requirement must be offset against the loss which may be sustained from reduced carcass quality. It therefore follows that it may be desirable to maximize growth rate at certain stages of the animal's life and deliberately to retard it at others.

It is usually assumed that rapid growth is desirable in breeding stock and on commonsense grounds it seems reasonable to suppose that a high plane of nutrition in early life would be the best preparation for the subsequent strain of pregnancy and lactation. However, there are two important considerations governing the rearing of female breeding stock, *viz.* the age at which the animal can be bred from for the first time and its life-time performance. The age at which an animal can be bred from for the first time is related to its age at puberty, and age at puberty is increased by retarded growth rate. Delayed breeding means that an animal must be kept longer, without any financial return, than one which can be bred from early, so that

from this point of view rapid growth and early puberty are desirable. On the other hand from the stand-point of life-time performance it has not been conclusively demonstrated that there is a close correlation between rapid growth rate and a good life-time performance. Very little work has been carried out on the factors which influence life-time performance and until these have been investigated it is impossible to say whether the high rate of wastage in, for example, dairy cows and brood sows, resulting from the incidence of disease and reproductive failure may not in part be a consequence of rapid growth rates. Some evidence on this point has been obtained by HANSSON and his co-workers (1953) using identical twin calves. Identical twins have the advantage over other pairs of animals for some experimental purposes in that the genetic variation between pairs is eliminated and any differences must be due to environment. Pairs of identical twin heifer calves which had been reared on different levels of nutrition were bred and then culled for low milk yield. The surviving animals were then carried on until culling was finally made necessary because of sterility or disease. It was found that the average length of life of the heifers reared on a low plane of nutrition was 95 months compared with 75 months for those reared on a high plane of nutrition.

FACTORS AFFECTING LIVE-WEIGHT GROWTH

(1) PLANE OF NUTRITION

The effect of plane of nutrition on live-weight growth is important agriculturally because of its relationship to the economics of meat and milk production. Changes in the growth rate of meat animals brought about by changes in plane of nutrition directly affect the rate of turnover and the efficiency of conversion of food into meat. Varying planes of nutrition at different stages of development also affect the composition and, therefore, the value of the carcass, so that a knowledge of the way in which the plane of nutrition affects growth enables the farmer to control, to some extent, the carcass quality of his meat animals. Alternatively, it enables him to take steps to ameliorate the adverse effects of natural recurrent periods of low plane nutrition such as occur in various parts of the world as a result of seasonal low rainfall.

Rearing an animal on a very high plane of nutrition means that nutrition ceases to be a limiting factor in growth rate, which consequently is limited by the genetic constitution of the individual animal. Rapid growth resulting from a high plane of nutrition means that an animal reaches a marketable weight in a minimum time but rapid growth is not necessarily most economic growth from the point of view of efficiency of food conversion. McMEEKAN (1940) fattened

GROWTH

pigs from shortly after birth to 200 lb live weight on four different planes of nutrition, *viz.*—

- (1) High plane throughout.
- (2) High plane to 16 weeks of age followed by low plane.
- (3) Low plane to 16 weeks of age followed by high plane.
- (4) Low plane throughout.

The plan of this experiment (*Figure 9.2*) had the somewhat unusual feature that the growth curves were predetermined and the animals in each group were made to grow along the appropriate growth curve

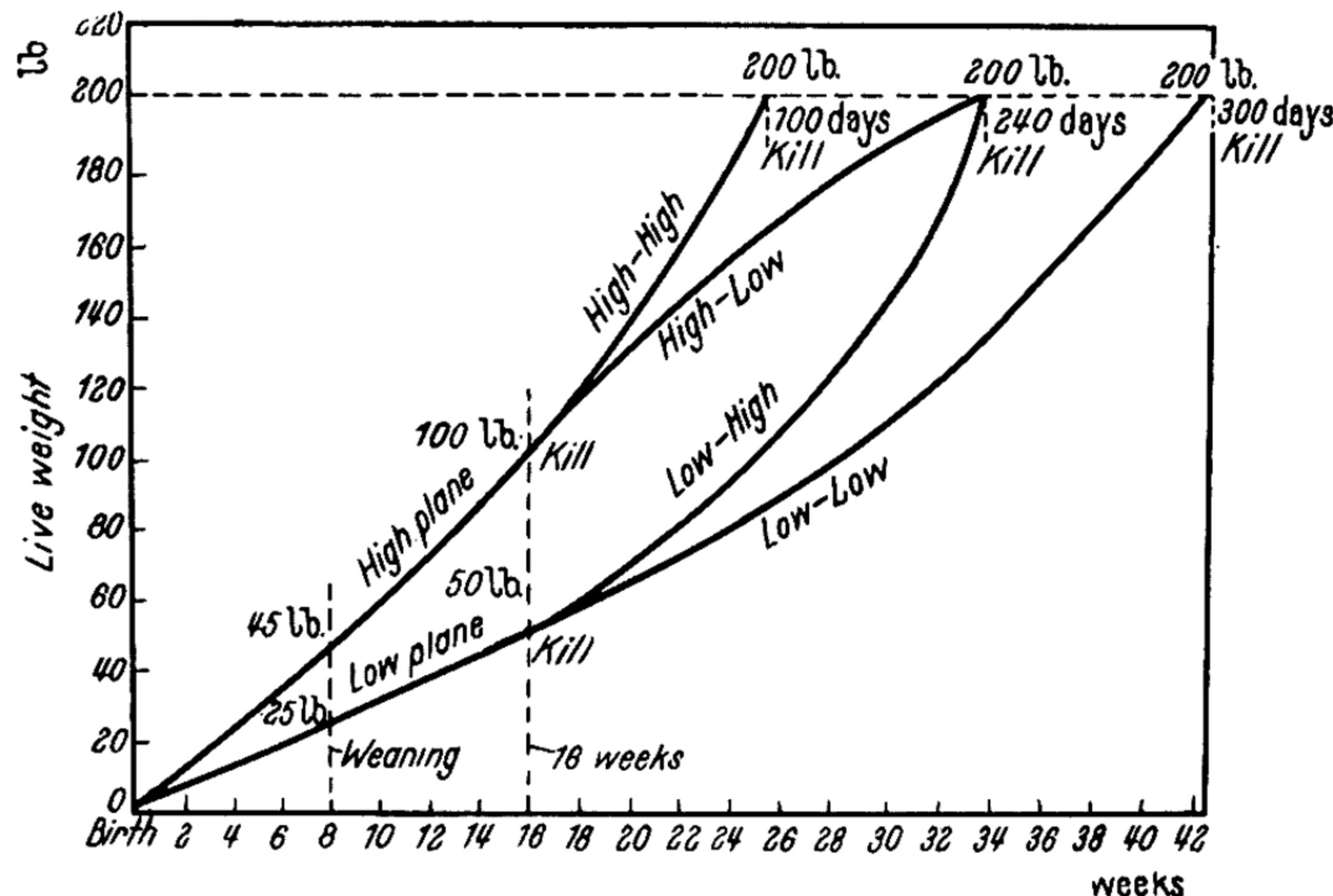


Figure 9.2. Plan of McMeekan's (1940) experiment to determine whether the conformation and composition of the pig can be changed by altering the shape of the growth curve by changes in the plane of nutrition (by courtesy *J. agric. Sci.*).

by regulating their food consumption. He found that the pigs fed on a high plane throughout their life were less efficient from the point of view of pounds of meal consumed per pound live-weight gain, than the pigs fed on a high plane of nutrition to 16 weeks of age and then on a low plane thereafter. The amount of meal consumed per pound live-weight gain from weaning to 200 lb live weight was 5.05 lb in the case of the pigs fed on a high plane throughout compared with 4.28 lb in the case of the pigs fed on a high plane to 16 weeks of age and on a low plane thereafter. The reason for this difference is probably to be found in the differential growth of the different tissues of the body. The 'High-Low' pigs were transferred to a low plane of nutrition at a stage when fat was the most rapidly growing tissue. The economy of conversion of food into fat is low, so that restriction of food intake at this stage improved the overall efficiency of food conversion. Conversely, the 'Low-High' pigs which were transferred

to a high plane of nutrition when growth of fat was most rapid had the lowest efficiency of food conversion, 5.61 lb of food per pound live-weight gain, of all the four groups. In the case of the pigs kept on a low plane of nutrition throughout, the efficiency of food conversion was poor, 5.17 lb of meal per pound live-weight gain, because they required a much longer time to reach 200 lb live weight and consequently a much higher proportion of their total food consumption was devoted to satisfying their maintenance requirements. An interesting point which emerges from this experiment is that, although long-term retardation of growth rate depresses the efficiency of food conversion because it increases total maintenance requirement, short-term retardation at the appropriate stage of development may actually improve the overall efficiency of food conversion through its differential effect on the different tissues, and so chemical composition of the body.

Similar results have been obtained with cattle by BROOKES and VINCETT (1950). Their experiments also involved four planes of nutrition, *viz.*—

- (1) High plane during calfhood (*i.e.* up to 8 months) followed by high plane.
- (2) High plane during calfhood followed by moderate plane.
- (3) Moderate plane during calfhood followed by high plane.
- (4) Moderate plane during calfhood followed by moderate plane.

All the cattle were slaughtered at a stage when it was estimated that they would have a carcass percentage of 57 per cent. The 'High-High' and 'Moderate-High' reached this stage in 2 years; the 'High-Moderates' in $2\frac{1}{2}$ years and the 'Moderate-Moderates' in $3\frac{1}{2}$ years. Although the 'High-High' cattle had the most rapid growth rate they were the least profitable because the rapid growth rate necessitated a high rate of feeding of expensive concentrated foods. The most profitable group was the 'High-Moderate' because the high plane of nutrition was supplied early in life when potential growth rate was high and the moderate plane was introduced when the growth rate was falling off. By this time, however, the growth made on the initial high plane of nutrition had enabled the animals to reach a size when they could make good use of cheap bulky foods. Consequently, although they had to be fed for a longer time the total cost was less because they were able to consume a greater proportion of cheap food.

The effect of under-feeding on growth in cattle was first studied by WATERS (1908) who kept young steers of different ages for a year on rations which permitted no gain in live weight. He noted that although live-weight growth was arrested skeletal growth was not,

and also that there was a very strong tendency towards recovery after the period of underfeeding ended. The recuperative capacity after a period of underfeeding was ascribed to a prolongation of the growth period, for it was noted that an animal which has been under-fed during early life will continue to grow after a normally fed animal has ceased to grow. ECKLES and SWETT (1918) working with dairy heifers noted a strong tendency to recover from retarded growth when conditions became favourable, but if the retardation had been carried too far the animals would not reach normal size. Recovery of growth was attributed partly to a prolongation of the growth period and partly to a greater than normal rate of growth on re-feeding.

The permanence of stunting following a period of under-nutrition has been disputed. Little conclusive evidence is available for the domestic animals largely because of the difficulty of keeping adequate numbers under controlled conditions for the long periods of time required for them to reach mature size. Consequently, most of the experimental work on the effect of under-nutrition on mature size has been carried out with small laboratory animals, notably the rat. Thus OSBORNE and MENDL (1915) showed that re-feeding rats after a period of retarded growth resulted in abnormally rapid growth and the rats ultimately reached normal mature size. This abnormally rapid growth after a period of under-nutrition is a constant feature of this type of experiment and is partly due to replacing fat in the cells of adipose tissue which have been depleted of their fat content by under-nutrition. However, it has also been suggested (RAGSDALE, 1934) that under-nutrition disturbs the normal relationship between chronological and physiological age in such a way that, in the case of an animal on a low plane of nutrition, physiological age proceeds at a slower rate. When animals whose growth has been retarded by under-nutrition are put on to a high plane of nutrition they tend to grow at a rate appropriate to their physiological age rather than a rate appropriate to their chronological age. Consequently, they grow faster than animals of the same chronological age whose growth has not been retarded.

McCAY and his co-workers in a series of experiments with rats in which growth was retarded by restricting calorie intake, showed that if growth was retarded for a period in excess of the normal life span the rats were still able to grow again on re-feeding, but failed to reach the normal adult size. In a typical experiment (McCay *et al.*, 1939), groups of rats were retarded in growth by restricted calorie intake for 300, 500, 700 and 1,000 days and then re-fed. Rats which had been retarded for 300 days failed to reach normal mature size but some of the rats retarded for as long as 1,000 days were still able to grow to some extent on re-feeding.

The ultimate effect on body weight of a period of retarded growth

probably depends on three main considerations. First, the effect depends on the stage of growth at which retardation is applied. Osborne and Mendl (1915) restricted growth at a late stage of growth whereas McCay (1939) restricted it at an early stage. This indicates that permanent stunting is more likely to result from a period of retarded growth, if the retardation is applied early in life, when growth rate is high, than if it is applied later in life when the growth rate is relatively low. Secondly, the effect of retarded growth is dependent on the severity of the retardation and, thirdly, on the length of time during which the retardation is imposed. The animal body shows considerable flexibility in recovering from a period of retarded growth, but if the retardation occurs early in life and if it is sufficiently severe and prolonged, permanent stunting may result.

The effect of restricted nutrition in very early life on growth of sheep has been pointed out by HAMMOND (1932), who showed that single lambs are about 29 per cent heavier at birth than twin lambs which, in turn, are about 9 per cent heavier than triplets. During the first month after birth the difference in size between singles and twins increases because during this period the lambs are entirely dependent on milk and in the case of twins the milk supplied by the ewe has to be divided between two lambs. Once the lambs start to eat solid food and become independent of the milk of the ewe, the growth rate of the twin lambs starts to overtake that of the singles, but during the period over which Hammond made his observations, *i.e.* 2 years, the difference in size between singles and twins was still apparent.

The milk supplied by the dam is an important factor in the post-natal growth of young mammals as can be seen if the growth of a young mammal like the rabbit is compared with the growth of the chick (Figure 9.3, from MURRAY, 1921). A similar picture is obtained by comparing the growth rates of pigeons and those of chicks

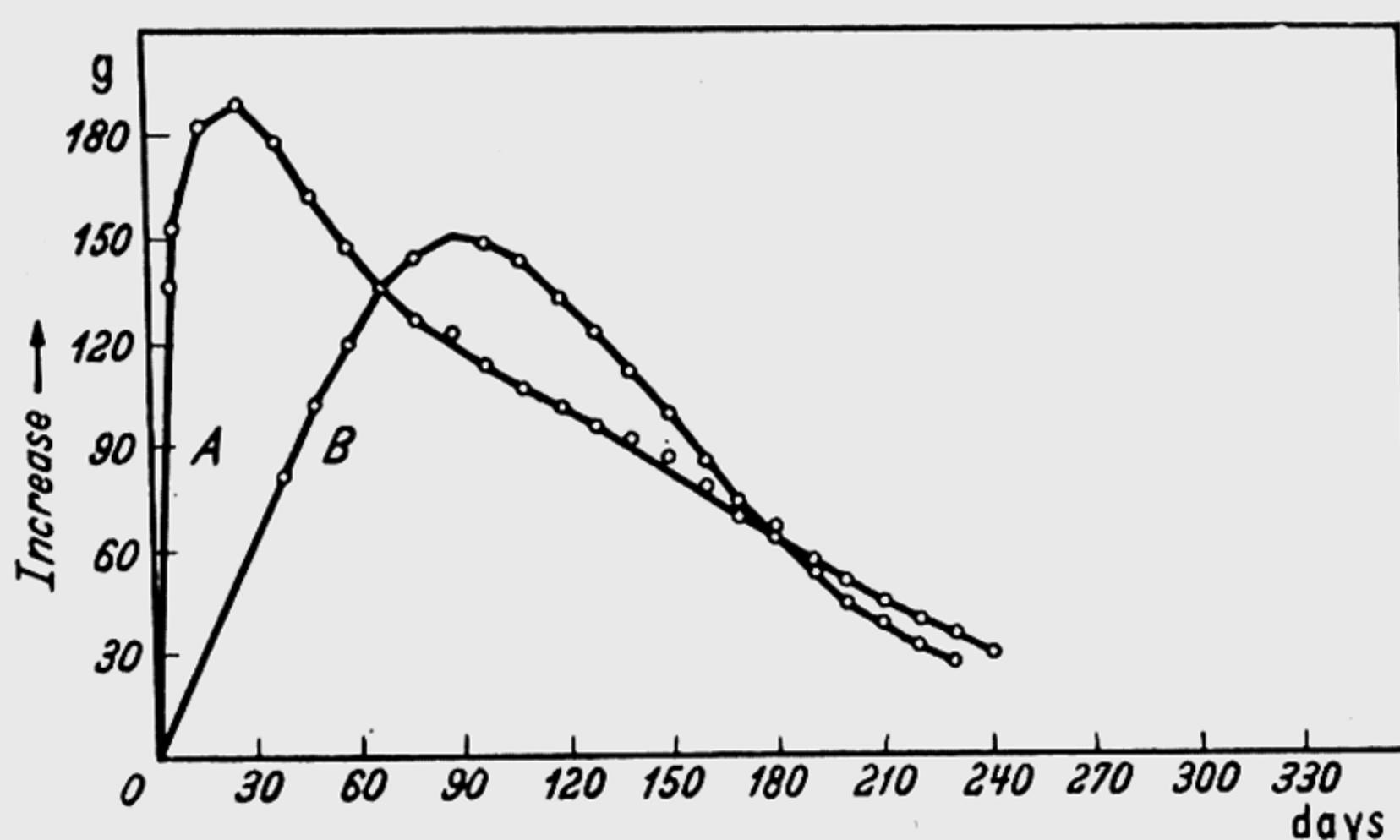


Figure 9.3. Comparative rate of growth (increase in grams/day) in rabbits (A) and chickens (B). (From Murray (1921), by courtesy *J. agric. Sci.*)

GROWTH

(Figure 9.4) (KAUFMANN, 1929). The young pigeon which receives 'milk' in the form of secretions from the crop gland grows over 300 per cent in the first month, whereas the chick grows only 160 per cent.

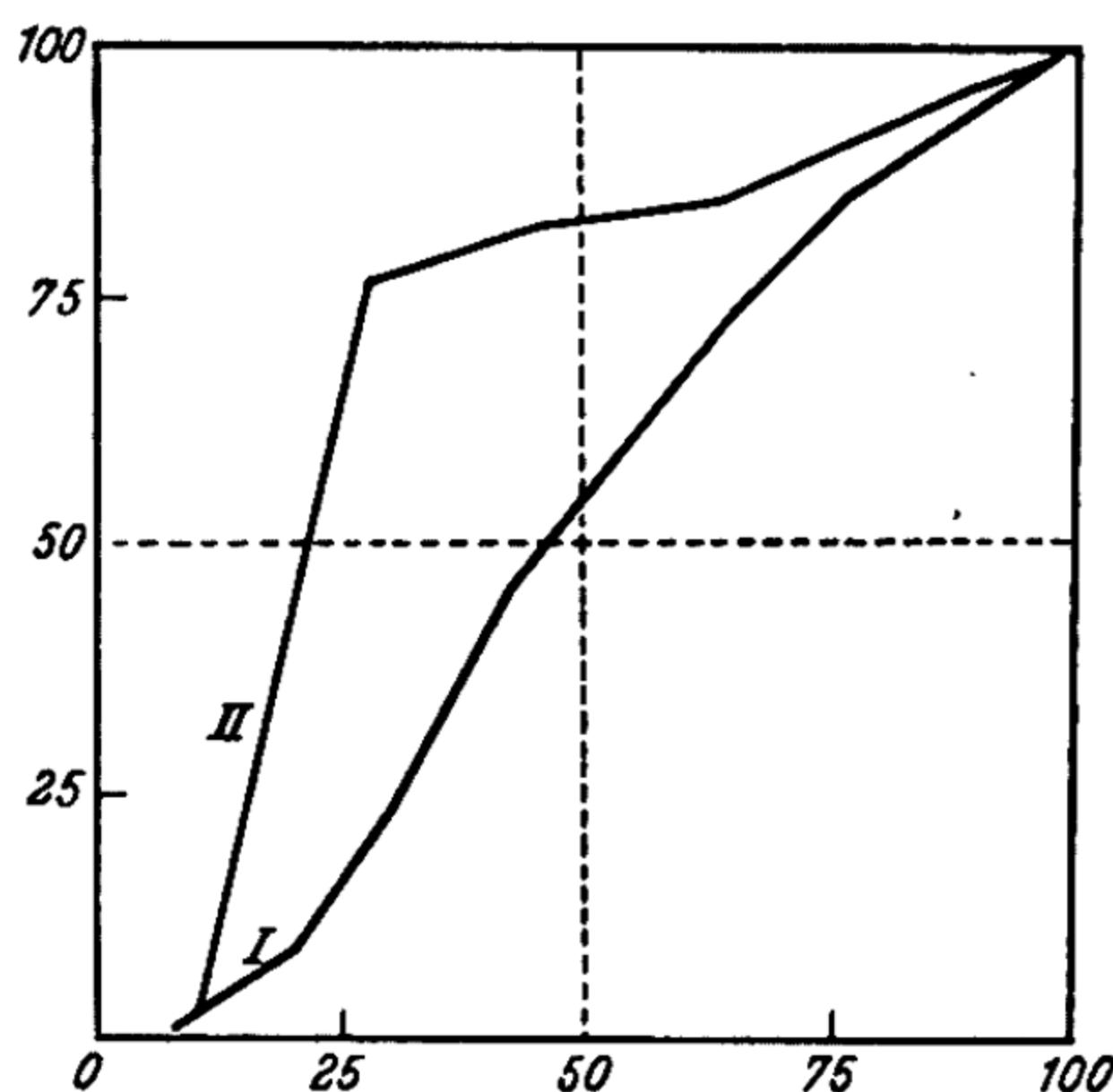


Figure 9.4. Comparative growth of young chicken (I) and pigeons (II). (From Hammond (1952), by courtesy Edward Arnold (Publishers) Ltd.)

WALLACE (1948) showed that the nutrition of the female during the late stages of pregnancy has a marked effect on milk yield largely through its influence on the growth of the udder (Figures 9.5 and 9.6).

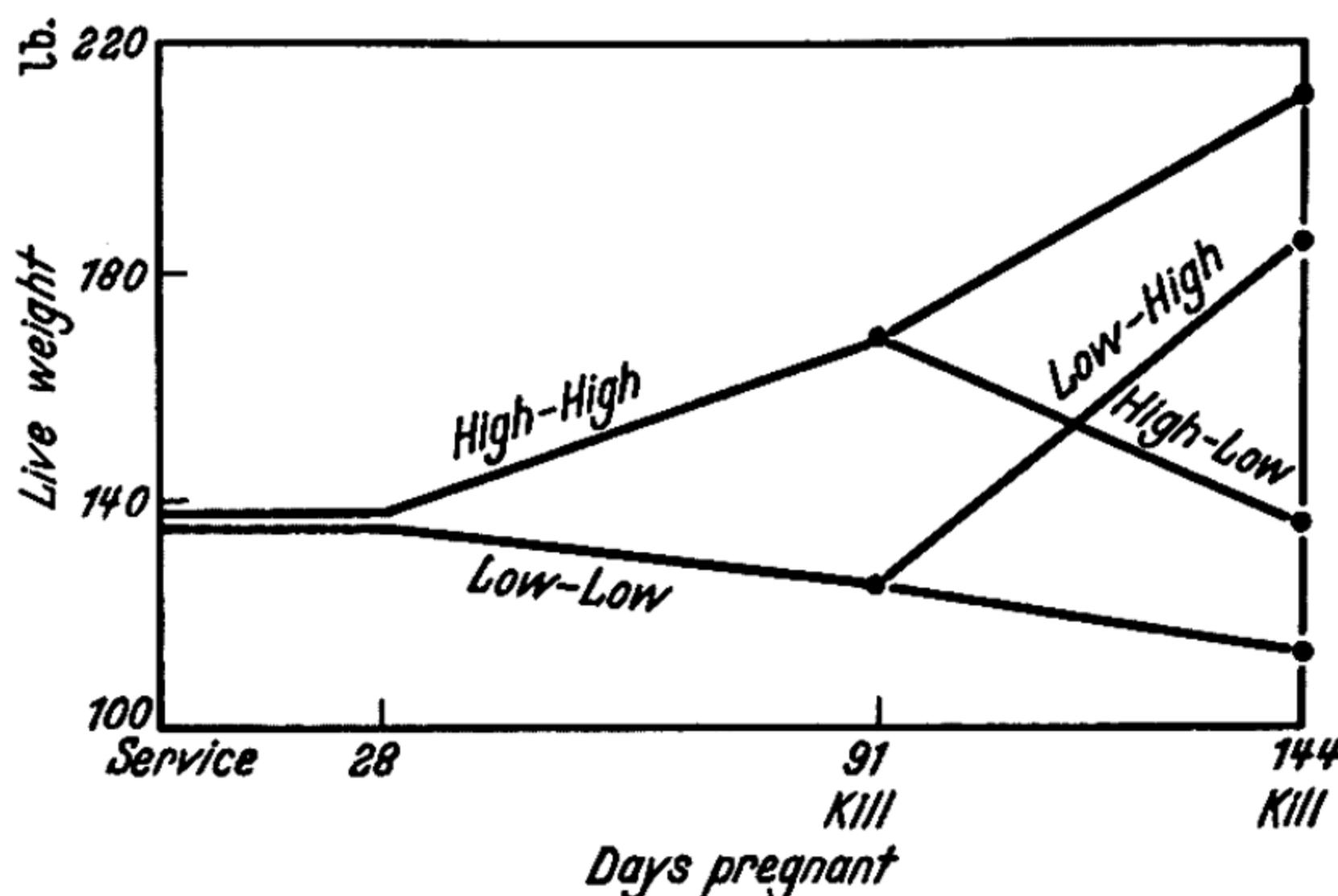


Figure 9.5. Growth curves of ewes during pregnancy. (From Wallace (1948), by courtesy *J. agric. Sci.*)

According to BONSMA and OOSTHUTZEN (1935) the milk yield of sows remains constant for litters of over seven to eight pigs. This fact largely accounts for the observations of JOHANSSON (1931-2) and KITCHIN (1937) that the average weight of pigs at weaning decreases with increasing litter size. It also emphasizes the desirability of feeding large litters well from the time they start to take solid food.

The retarding effect on growth of restricted nutrition prenatally is shown by the fact that the growth rate of twin lambs reared as

LIVE-WEIGHT GROWTH

singles, while greater than that of twins reared as twins is less than that of singles reared as singles (Hammond, 1932). Wallace (1948) has shown that the level of nutrition of the ewe during the later stages of pregnancy has a marked effect on the weight of the lamb at birth.

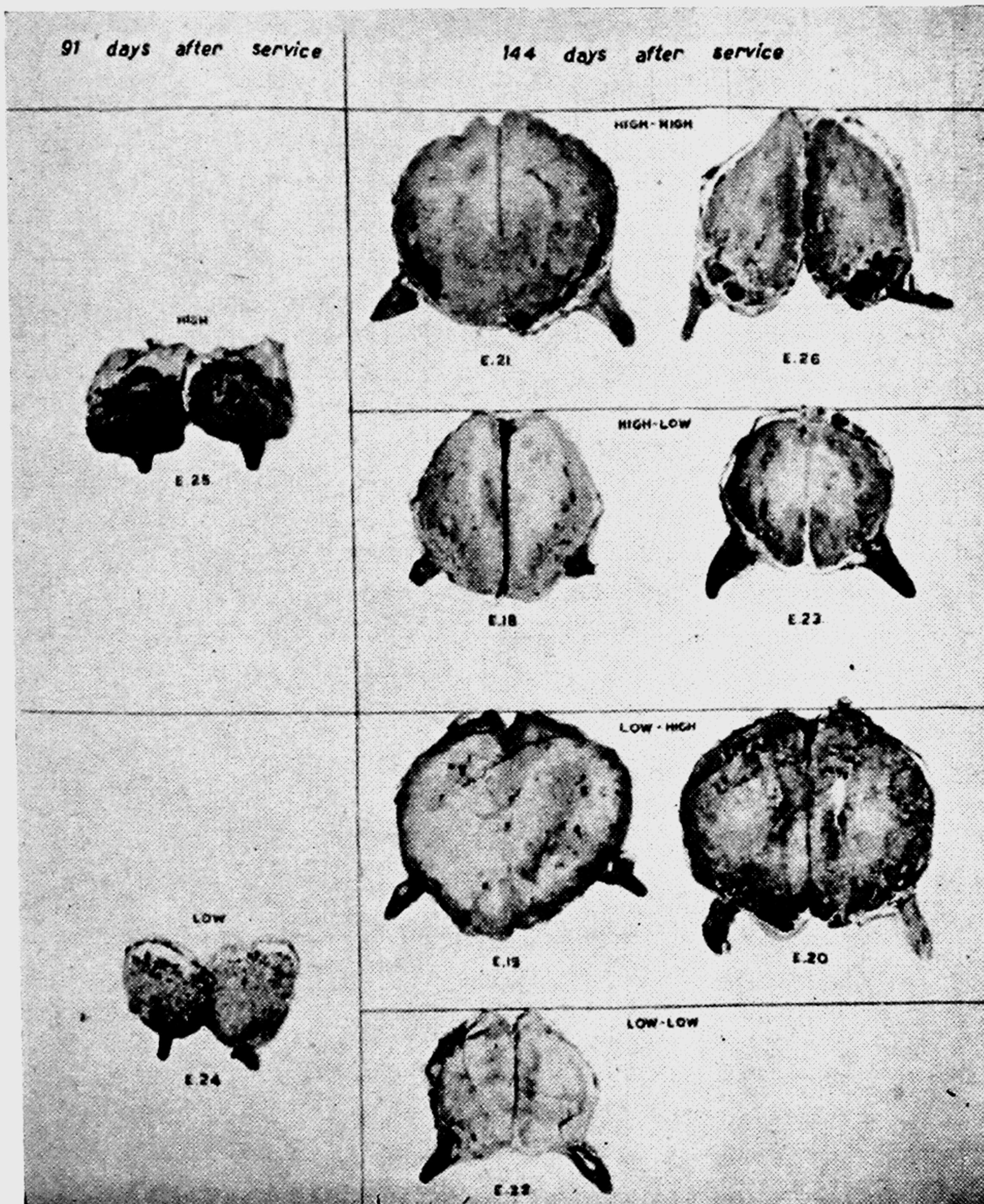


Figure 9.6. Effect of plane of nutrition of ewe (see figure 9.5) on growth of udder. (From Wallace (1948), by courtesy *J. agric. Sci.*)

Under-nutrition of the ewe during this period leads to the production of under-sized and weakly lambs even though the nutrition of the ewe earlier in pregnancy was on a high level. Conversely, a high level of nutrition of the ewe in late pregnancy resulted in normal

sized lambs even though the level of nutrition of the ewe in early pregnancy had been low (*Figure 9.7*).

Thus it would appear that the growth of the foetal lamb is to a great extent dependent on an adequate supply of incoming nutrients and the ewe is unable to compensate for a deficiency of dietary nutrients by drawing on her own reserves.

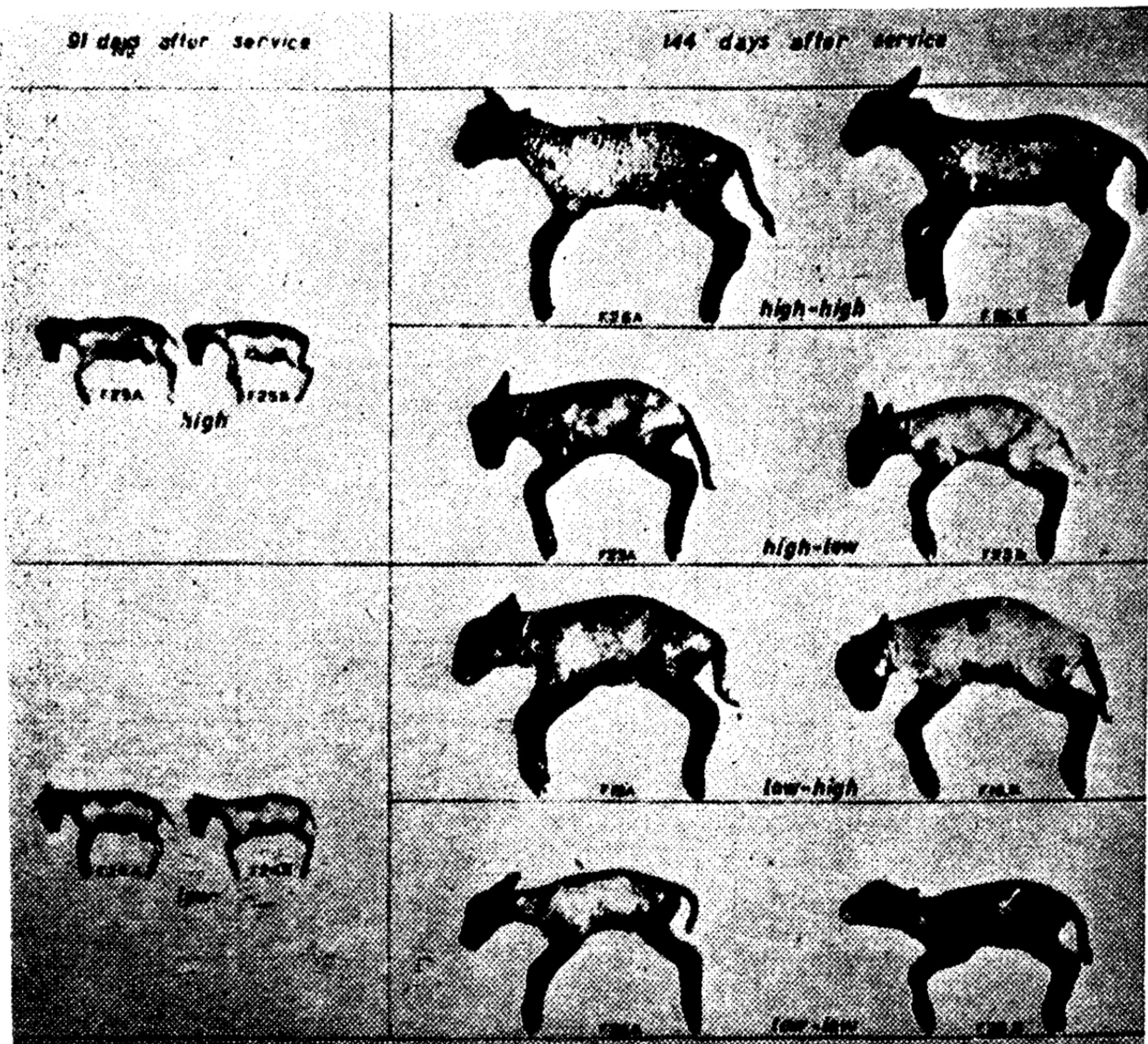


Figure 9.7. Effect of plane of nutrition of ewe on growth of lamb. (From Wallace (1948), by courtesy *J. agric. Sci.*)

Many of the undersized lambs died shortly after birth and an important factor in causing death was, apparently, a failure of the temperature regulating mechanism. It has been argued that animals which are undersized at birth are 'anatomically and physiologically premature' and that death results from the inability of the physiologically premature animal to withstand stress in a new environment. While there may well be some substance in this argument the exact implications of the concept of physiological prematurity have not been very clearly defined.

An extreme case of the effect of prenatal influence on postnatal growth is provided by the reciprocal crosses between Shire horses and Shetland ponies (*Figure 9.8*) made by WALTON and HAMMOND (1938).

At birth the cross-bred foal from the Shire mare was three times as large as the cross-bred foal from the Shetland mare. After birth the difference between the reciprocal crosses diminished, but it was still well marked after four years, at which time the weight of the foal from the Shire mare was still one and a half times that of the

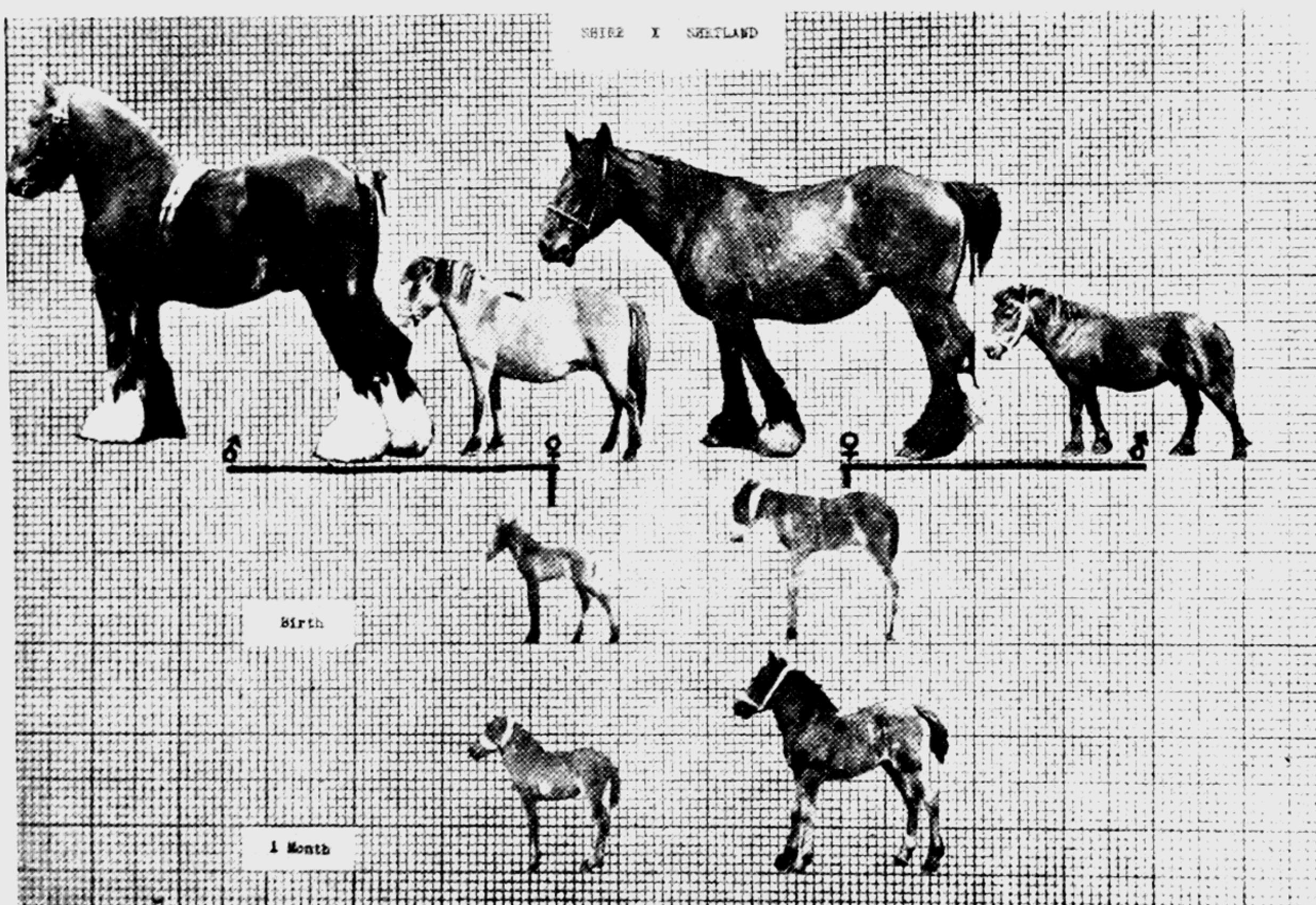


Figure 9.8. Maternal effect on the size of the foal in reciprocal crosses between the large Shire horse and small Shetland pony. (From Walton and Hammond (1938), by courtesy *Proc. roy. Soc. B.*)

foal from the Shetland mare. VENGE (1948) has shown a similar maternal influence in reciprocal crosses between large and small breeds of rabbits but here the difference was less marked than in the reciprocal crosses between horses and ponies possibly because gestation is relatively shorter in the rabbit than in the horse and the influence of the maternal environment is correspondingly less.

The effect on postnatal growth of nutrition in early life and particularly prenatal life, becomes important in those meat animals which are slaughtered when they are very immature. For example, in the case of the pork pig the prenatal period may represent half its total life from conception to slaughter and consequently prenatal influence is likely to be of greater relative importance than in the beef steer, where the prenatal period is only about 20 per cent of the life span. (For other factors affecting birth weight, see Chapter 10.)

The effects of recurrent periods of under-nutrition are of particular importance in countries like South Africa, Australia and America

where cattle are kept under range conditions and where the productivity of pastures is limited by seasonal low rainfall. Under such conditions live-weight growth is seasonal and parallel to the curve of monthly rainfall, with a time lag between the period of maximum rainfall and the period of maximum growth (SCHUTTE, 1935). It was not certain whether permanent stunting resulted from periodic under-nutrition but retarded growth led to a delay in reaching market weight. RAATH (1941) showed that steers which had to depend entirely on pasture lost weight during the period of low rainfall, but if they were given supplementary food they made uniform gains all the year round and the delay in reaching market weight due to seasonal under-nutrition was avoided.

It is well known that when improved British breeds of cattle are exported to tropical or sub-tropical countries they rapidly deteriorate and their performance may be no better, and is frequently worse, than that of indigenous breeds. This is obviously partly a question of resistance to tropical diseases and parasites, but over and above this are the problems of seasonal under-nutrition, high temperature and the interaction of high temperature and plane of nutrition. These problems have been investigated in South Africa by JOUBERT (1954) using Afrikaner and Shorthorn beef cattle and Friesian and Jersey dairy cattle. The climatic conditions were such that pasture was abundant in summer and scarce in winter, and under these conditions the relative growth rate of the Beef Shorthorns tended to be better than the Afrikaners during the winter, but worse during the summer. The reason for this was that summer temperatures were so high that the Beef Shorthorn was unable to graze, even though pasture was abundant, whereas the indigenous Afrikaner, not being affected by the high temperature, was able to continue to graze. In winter, on the other hand, when temperatures were lower, the Beef Shorthorn was also able to graze and then, although food was limited, the superior growth capacity of the Beef Shorthorn could express itself. The Shorthorn is inherently a quicker maturing breed than the Afrikaner and it was found that when animals of both breeds were reared on high and low planes of nutrition the differences between Shorthorns on high and low planes of nutrition tended to increase with advancing age while the differences between Afrikaners on high and low planes of nutrition tended to decrease. This indicates that temporary lowering of the nutritional level inflicts more permanent damage to early maturing animals than to late maturing animals.

A comparison between the growth rates of Friesian and Jersey cattle showed that the Jerseys did not have as great seasonal variations in weight under adverse conditions. This is partly due to the superior heat tolerance of the Jersey and partly to the fact that the Friesian, being a much larger breed than the Jersey, has a correspondingly

LIVE-WEIGHT GROWTH

greater maintenance requirement and is consequently affected to a relatively greater extent by periods of under-nutrition.

During the course of these experiments Joubert recorded an extensive series of body measurements which were later correlated with live-weight growth. He confirmed the earlier observation of LUSH *et al.* (1930) and RAGSDALE and BRODY (1935) that the only measurement which gives a close correlation with live-weight growth is chest girth. The reason for this appears to be that most of the measurements which can be recorded with a reasonable degree of accuracy, such as length of body or height at shoulder, are really measures of bone growth and since bone is an early developing tissue it is relatively insensitive to variations in plane of nutrition. Chest girth, on the other hand, is a measure of development of muscle and fat as well as of bone, and as such it is more sensitive to variations in plane of nutrition.

(2) SEX

The effect of sex on live-weight growth is two-fold. First, there is a direct effect of sex on growth resulting presumably from genetic

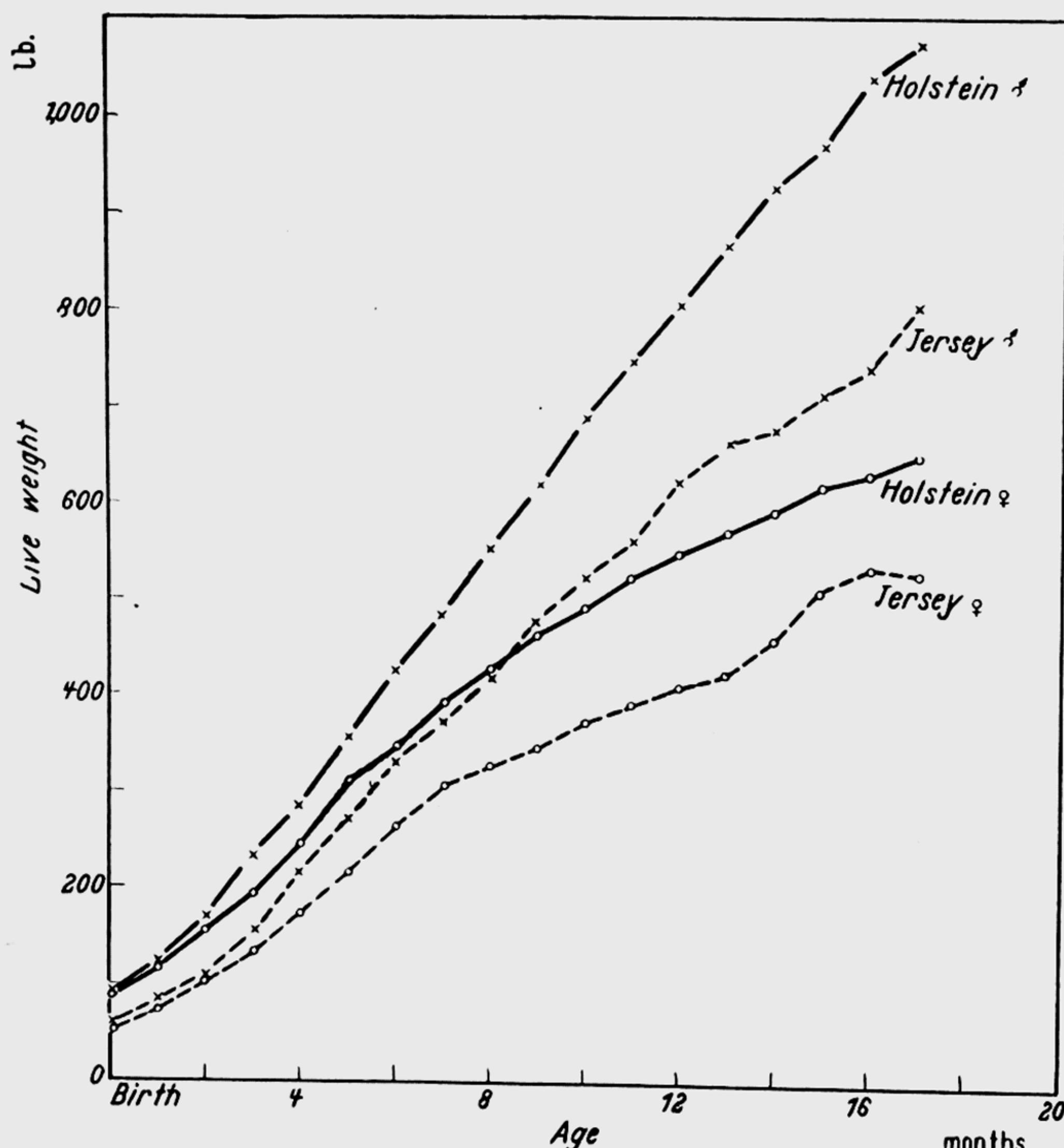


Figure 9.9. Growth of male and female cattle from birth to 17 months.
(Redrawn from data by Ragsdale, Elting and Brody.)

GROWTH

differences between males and females, and secondly there is an indirect effect of sex due to the influence of the sex hormones.

In most mammals and birds, males tend to grow faster and reach heavier weights than females, but, as Hammond (1932) pointed out, figures quoted for relative weights of bulls and cows and rams and ewes, need critical examination, for the tendency in both cattle and sheep is for males to be better selected and better fed than females. Thus, some of the difference between figures quoted for mature weights of bulls and cows may be due to differences in genetic constitution or in plane of nutrition, rather than to sex differences. Furthermore, in the case of sheep, account must be taken of the difference in growth rate between the growth rate of singles and twins since it would obviously be misleading to compare the growth rate of rams born as singles with that of ewes born as twins.

Nevertheless, after allowing for these possibilities there appear to be real sex differences in live-weight growth which vary in different species. Thus in cattle (*Figure 9.9*) and sheep (*Figure 9.10*) males are heavier than females at birth and this difference persists throughout life. In horses, on the other hand, there is no appreciable difference between the sexes at birth nor for some time after birth. Thus OLSSON (1952) showed that there was no appreciable difference between males and females up to 17 months after birth but thereafter males grew faster than females (*Figure 9.11*).

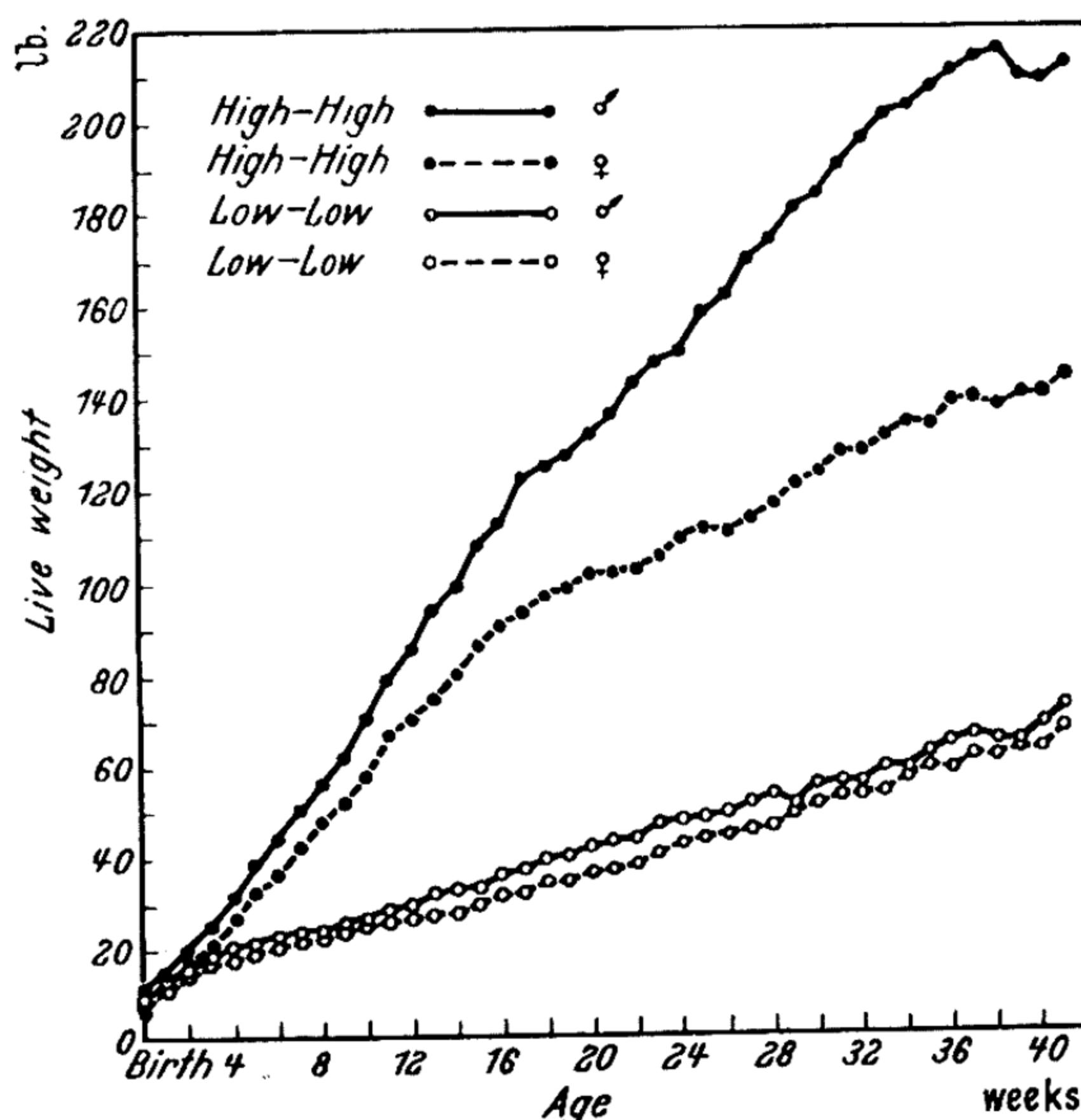


Figure 9.10. Growth of male and female sheep reared on High and Low Planes of nutrition. (From Pálsson and Vergés, (1952), by courtesy *J. agric. Sci.*)

LIVE-WEIGHT GROWTH

Figure 9.10 from PÁLSSON and VERGÉS (1952) shows that the difference in growth rate between the sexes in sheep is apparent only when the nutritional régime on which the animals are reared is adequate for normal growth and when lambs were reared on a low plane of nutrition there was virtually no difference between the growth rate of males and females.

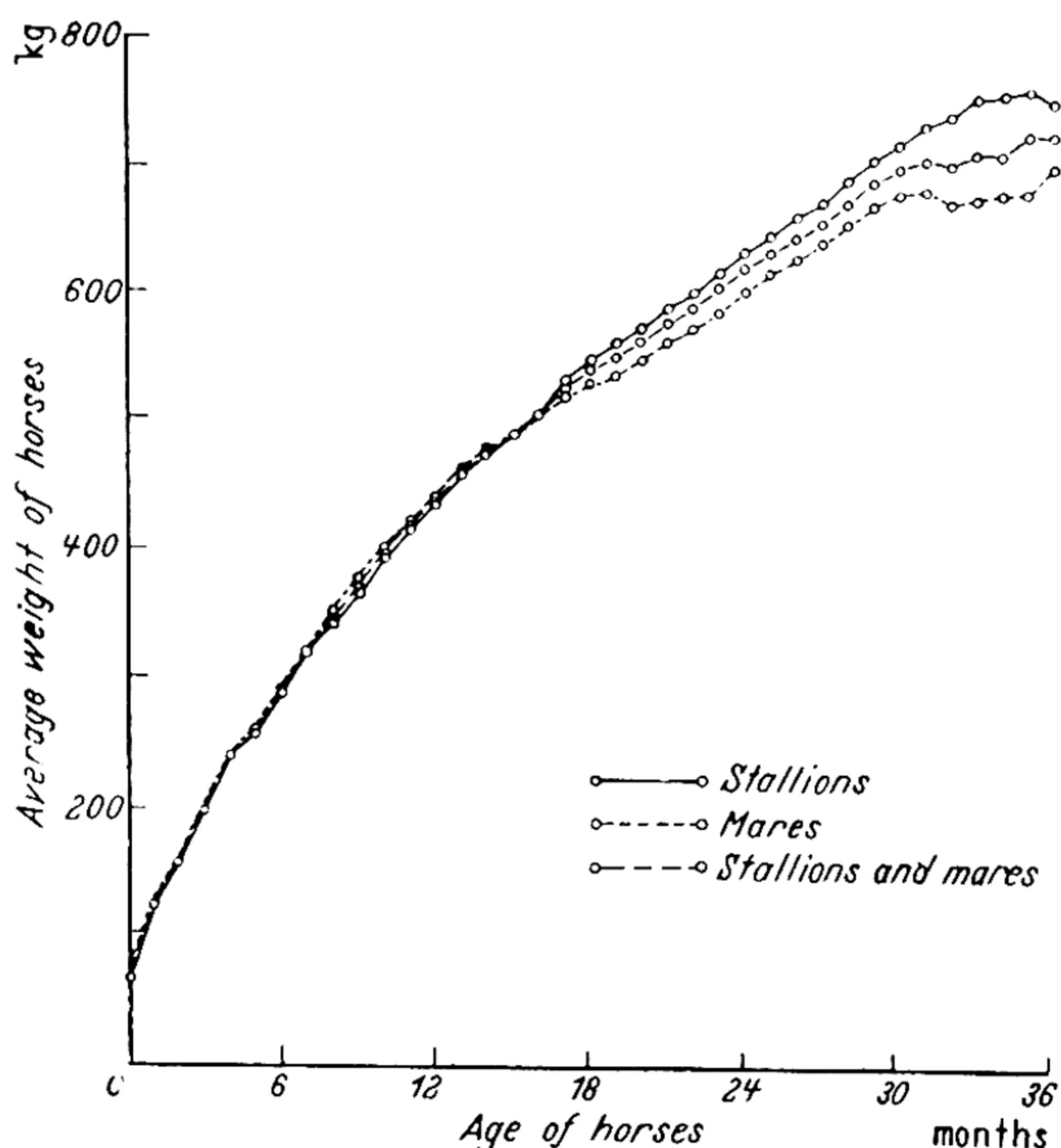


Figure 9.11. Growth of male and female horses (Belgian) from birth to 3 years. (From Olsson (1952), by courtesy *Statens Husdjursforsok Medd.*)

In poultry WILSON (1952) has shown that there is no difference in weight between the sexes at birth but cockerels grow faster than hens and to a greater mature weight. It has been shown by FINLAY (1925) and by ZAWADOWSKY (1931) that castrating a cockerel produces a bird which lacks the male secondary characters, comb, wattles and spurs but is larger and heavier than the hen. Similarly, castrating hens produces a bird which is no larger or heavier than a normal hen. If ovaries are transplanted into castrated cockerels the resulting birds have the appearance of a normal hen but are of the same weight and size as a normal cockerel. Whereas if testes are transplanted into castrated hens, the birds have the appearance of a normal cockerel but are of the same size and weight as a normal hen (*Figure 9.12*). Thus in poultry the difference in growth rate between the sexes is primarily a genetic difference and not due to the influence of the sex hormones.

(3) HORMONES

The literature relating to the effects of hormones on various physiological functions, including growth, is extensive and tends to be confusing. Confusion arises from a number of causes. Hormones do not act independently but as part of a complex pattern. Consequently experiments involving extirpation of an endocrine organ or

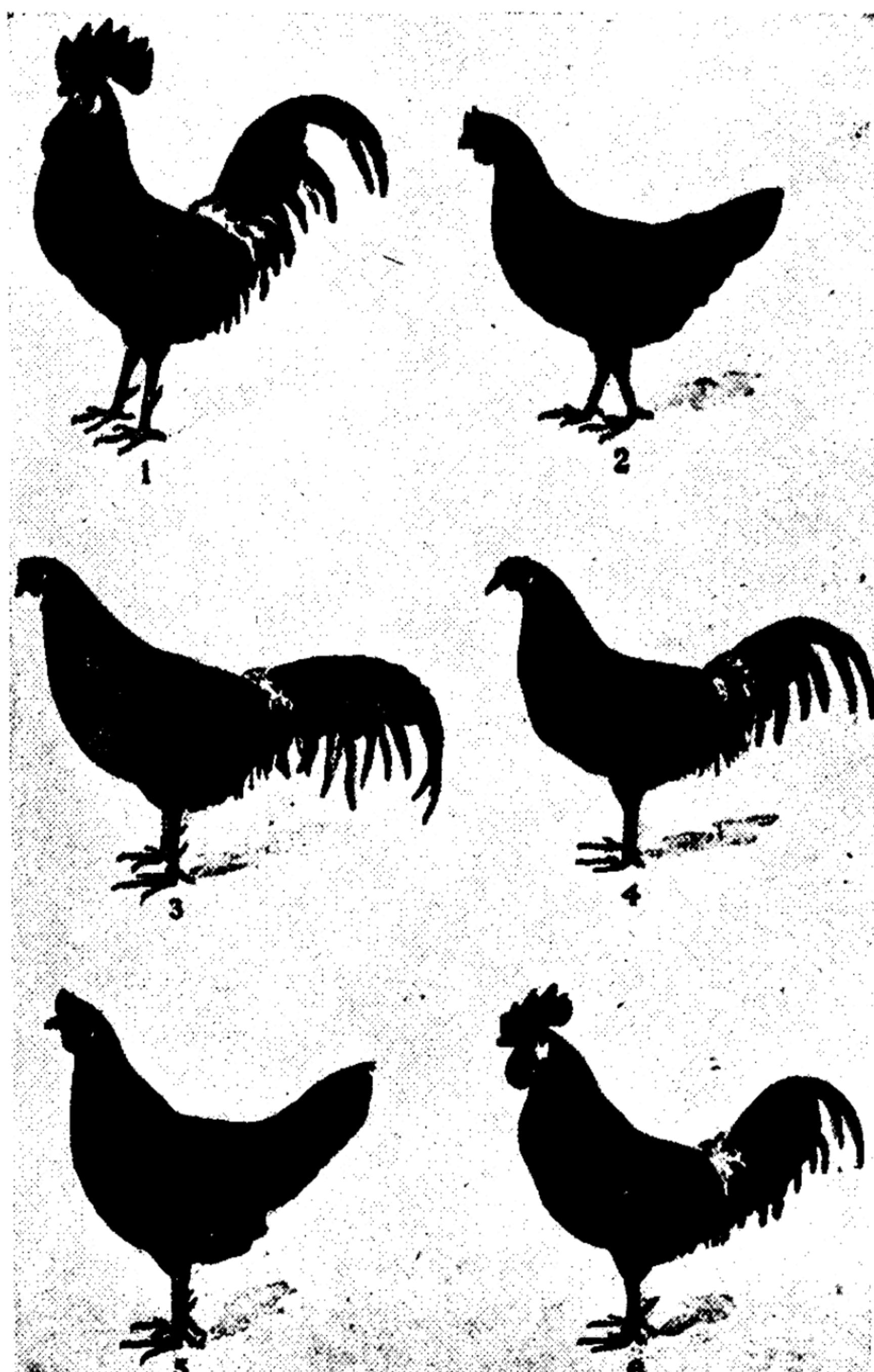


Figure 9.12. Sexual differences in size in Brown Leghorn fowls. (From Hammond (1952), by courtesy Edward Arnold (Publishers) Ltd.)

injection of endocrine extracts can produce variable and sometimes conflicting results, depending on the reactions of the rest of the endocrine system. Some glands such as the pituitary and the adrenal cortex produce a number of hormones which have not yet been completely isolated and purified; for example, the adrenal cortex is believed to produce at least twenty different hormones. Consequently the variable results reported by different investigators may

be due, in part, to their using variable mixtures of hormones. In fact, the hormone preparations frequently used may be only degradation products of the hormones actually produced by the glands.

In general, the line of attack in endocrinology has been first of all to study the effects of extirpating a particular gland. Then the effects have been observed of administering extracts of the gland to intact animals and to animals from which the gland has previously been extirpated. This has been followed by attempts to purify and determine the chemical composition of the hormones produced by the gland. Very little is known of the precise mode of action of hormones and until further progress is made in this direction the picture is likely to remain somewhat confused.

Until recent years most hormone preparations were made from natural sources, *i.e.* the endocrine glands of animals. Such preparations are expensive to produce and, as a result, much of the experimental work that has been carried out with hormones in relation to growth has been done with small laboratory animals such as the rat. The production of synthetic oestrogens and synthetic thyroprotein has, to some extent, facilitated research with larger animals but the large scale application of hormone preparations to the study of growth in farm animals is still not a practical possibility. However, it is probably true that the broad principles which have been discovered as a result of experiments with small laboratory animals are, in the main, applicable to domestic animals. With these considerations in mind it is possible to review some of the results which have been obtained with various hormones in relation to growth.

Sex Hormones

The difference in growth rate between the sexes is present not only post-pubertally but also pre-pubertally and even prenatally (HILL, 1939). In the case of females it has been shown that the administration of oestrogens to normal females for a prolonged period inhibits growth by inhibiting growth of the long bones (SPENCER *et al.*, 1931; ZONDEK, 1936). This inhibition of growth of the long bones is brought about by ossification of the epiphyseal cartilages. COLE and HART (1938) showed that, in rats, pregnancy resulted in increased growth above that of non-bred litter mate controls. The excess growth rate resulting from pregnancy was maintained at a fairly constant rate for the first six pregnancies after which subsequent pregnancies had less effect. The increase in growth rate was ascribed to increased appetite. BOGART *et al.* (1940) showed that ovariectomized female rats grew more rapidly than virgin rats but both reached a plateau in their growth curves at the same age. Rats which were bred but not allowed to lactate grew faster than virgin rats, and for a longer time. Females which were allowed to lactate also grew

faster than virgins but not so fast as females which were bred but not allowed to lactate. It was suggested that in virgin rats growth is inhibited by oestrogens secreted by the ovaries and that the increased growth following ovariectomy is directly due to the removal of the inhibiting influence of oestrogen. The increased growth during pregnancy was ascribed to the removal of the inhibiting influence of oestrogen through the mediation of the corpus luteum. It was later shown by BOGART, LASLEY and MAYER (1944) that injected oestrogen would inhibit growth in normal and ovariectomized rats and that conversely progesterone stimulated growth. Progesterone resulted in increased growth whether it was given directly or produced systemically by the injection of lutealizing hormone, by pseudopregnancy or by true pregnancy. It was noted, however, that the increased growth resulting from pregnancy was greater than that produced by the administration of progesterone alone. The reason for this is not very clear but a possible explanation might be that progesterone is very rapidly eliminated from the body and hence it is difficult to keep up a controlled level of progesterone by repeated injections, whereas the corpus luteum of pregnancy is presumably secreting continuously.

Females that are bred early in life and allowed to lactate may actually suffer a retardation in growth over a combined pregnancy and lactation, because the retarding effect of lactation may outweigh the growth stimulus due to pregnancy. Nevertheless, females which are bred from early in life reach the same mature size as those bred at the normal time, but females bred late in life do not reach the same mature size because in this case the growth stimulus due to pregnancy is less effective as it comes at a time when growth rate is diminishing.

Contrary to the stimulus to growth obtained with progesterone and the inhibition obtained with oestrogens, it has not been possible to produce any very appreciable effect on growth rate by the use of testosterone. McEUEN, SELYE and COLLIP (1937) treated rats with graded doses of testosterone but even very large doses which were sufficient to inhibit the development of the gonads failed to produce any marked effect on the growth rate.

With the production of the relatively cheap synthetic oestrogens, stilboestrol and its derivatives, it became feasible to carry out experiments on the effects of administering oestrogens on the growth rate and carcass quality of meat animals. Many such experiments have been repeated, but the results are somewhat conflicting. Thus DINUSSON, KLOSTERMAN and BUCHANAN (1951) found that 12 mg tablets of stilboestrol implanted subcutaneously in pigs did not produce any appreciable stimulus to growth rate, but it improved the efficiency of food conversion. On the other hand WOEHLING *et al.*

(1951) in a similar experiment failed to detect any hormonal control of growth or fattening. With fattening lambs, MEANS, ANDREWS and BEESON (1953) and O'MARY *et al.* (1952) found that stilboestrol implanted subcutaneously improved the rate of live-weight gain and the efficiency of food conversion. However, the dressing percentage and carcass quality were consistently reduced. In the latter case the proportion of bone and connective tissue was increased and the amount of external fat decreased. The exact mode of action of exogenous oestrogens in stimulating growth rate has not been very clearly established but it may be that inhibiting the secretion of gonadotrophic hormones by the anterior pituitary alters the balance of gonadotrophin-somatotrophin in favour of the latter.

Thyroid

The thyroid gland is primarily concerned with the regulation of energy metabolism. The effects of hypofunction of the gland in producing cretinism in the young and myxoedema in adults are well known in humans.

In young animals removal of the thyroid has been shown to retard growth in weight and the mature weight of thyroidectomized individuals has been shown to be only about half that of normal adults (BRODY and FRANKENBACH, 1942). Hypothyroidism is associated with low metabolic rate, reduced feed intake, low blood sugar and liver glycogen and low nitrogen retention. There is a tendency towards increased deposition of fat and it is this fact which has formed the basis of numerous experiments on the effect of partial thyroidectomy and on the effect of anti-thyroid drugs, notably thiouracil and thiourea, on the fattening of farm animals. ANDREWS and BULLARD (1940) subjected steers weighing between 435 lb and 900 lb to partial thyroidectomy. There was some loss in weight following the operation, but after the animals had recovered their pre-operative weights there were further rapid gains in weight for the following six weeks. This was ascribed to decreased metabolic rate following partial thyroidectomy. After the six weeks period of rapid live-weight gain the rate of gain declined probably as a result of hypertrophy of the remaining thyroid tissue. ZORN and BRUGGEMANN (1939) found an improvement in the rate of fattening of pigs thyroidectomized at weights between 20 and 30 kg but not at higher weights.

Variable results have been obtained with the use of anti-thyroid drugs, such as thiouracil and thiourea. This variability is partly due to the very variable response of individual animals and also to lack of appreciation of the sensitivity of the thyroid gland, so that in many cases what was intended to be mild hypothyroidism was, in fact, severe hypothyroidism. BRATZLER, BARNES and SWIFT (1949) found that rats receiving 0.1 and 0.2 per cent respectively of thiouracil in

their rations gained respectively 1.7 and 2.2 times as much body weight as rats on the same diet without thiouracil during a 16-week feeding trial; the differences in the gains of body weight being mainly in the form of fat. In the case of pigs WILLMAN *et al.* (1949) found that 0.1 per cent of thiouracil included in the ration fed *ad lib.* in a self-feeder to growing pigs depressed the rate of gain and efficiency of food conversion. However, when 0.2 per cent of thiouracil was included in a ration fed as a slop, the pigs receiving thiouracil made greater and more economical gains than the control pigs for the first 28 days but from the 28th day onward the rate of gain was low and the efficiency of food conversion was poor. Hand feeding to appetite, with a ration containing 0.1 per cent thiouracil resulted in more economical live-weight gains but not in faster growth than in control pigs. Again after 28 days both the rate of gain and the efficiency of food conversion of the pigs receiving thiouracil was depressed. On the basis of these results it was concluded that thiouracil might be useful in improving the rate of fattening of pigs if included in the ration for only limited periods. Somewhat similar conclusions were arrived at by VANDER Noot *et al.* (1948), who advised that thiouracil should not be fed to pigs until they have reached the desired stage of skeletal development; but after this stage the inclusion of 0.25 per cent of thiouracil in the diet increased the daily rate of live-weight gain and improved the efficiency of food conversion. On the other hand BERGE and GJELSTAD (1951) found that 0.1 per cent of thiouracil in the ration of fattening pigs depressed both the rate of gain and efficiency of food conversion. When the proportion of thiouracil was reduced to 0.05 per cent of the ration, the rate of gain and efficiency of food conversion was about the same as in the control pig. A consistent feature of all the experiments on feeding thiouracil to fattening pigs is that any increased live weight gains compared with the control pigs consist very largely of fat. Thus even if thiouracil consistently improved rate of gain and efficiency of food conversion it could only have a practical application in countries where the lard type of pig is produced. Under British conditions where there is a general tendency for the type of pig produced under normal conditions to be overfat in relation to consumer requirements, the feeding of the thiouracil would be definitely harmful.

The effect of hyperthyroidism is to increase metabolic rate and in severe hyperthyroidism catabolism exceeds anabolism, so that the effect of hyperthyroidism is to produce a loss of body weight. This effect can be produced in normal animals by administering the active principle of thyroid gland, thyroxine, or the more recently produced synthetic thyroproteins such as iodinated casein. Apart from causing loss of body weight continuous administration of thyroxine leads to adrenal hypertrophy (REFORZO-MEMBRIVES, 1943), damage to the

renal and hepatic circulatory systems (DRILL and HAYS, 1942) and an accelerated rate of senescence (SILBERBERG, 1943). However, in the case of farm animals the long-term deleterious effects of administration of thyroxine or synthetic thyroprotein must be balanced against any short-term advantages which may be derived from such administration. Thus in the pig, which is normally slaughtered when it is six or seven months old, the possibility of ultimate damage to the circulatory system is of no consequence, since the pig is slaughtered before the damage can be produced.

Although severe hyperthyroidism has a markedly adverse effect on live-weight growth, it is possible that mild hyperthyroidism might have a beneficial effect. Thus, MOLITCH and POLIAKOFF (1938) treated 43 boys of subnormal stature but with no definite clinical signs of hypothyroidism with 1 gram of thyroid gland per day and obtained an average growth of 1.25 inches in 6 months, compared with 0.75 inch in untreated controls.

Physiologically there appears to be an optimal dosage level for thyroxine. Below this level, administration of thyroxine suppresses the secretion of the animal's own thyroid gland to such an extent that the combined amount of exogenous and endogenous thyroxine remains unchanged. Above the optimal level, catabolism exceeds anabolism with consequent loss of weight and emaciation, while at very high levels thyroxine becomes definitely toxic. It has been pointed out by McCANCE (1953) that, while in the normal animal, food intake is attuned to energy output, in cases of thyrotoxicosis the regulation of food intake breaks down and the increased metabolism in thyrotoxicosis is not normally accompanied by increased food intake. Between these two extremes is a limited range within which administration of thyroxine may be capable of producing a favourable response in terms of live-weight gain. The physiologically optimal dosage level varies with the individual, with species, age, sex and environmental temperature. Much of the variability in response obtained in experiments on the administration of thyroxine to normal animals is attributable to variations in these factors and to failure to appreciate the sensitivity of the body to thyroid administration. In some cases the hyperthyroidism produced, though sub-toxic, was nevertheless severe.

In experiments on the administration of synthetic thyroprotein to pigs BEESON *et al.* (1947) and REINEKE *et al.* (1948) obtained significant increases in growth rate when synthetic thyroprotein was included in the ration. On the other hand VANDER NOOT *et al.* (1948) reported no increase in growth rate with small doses of thyroprotein and an actual decrease in growth rate with large doses. A fundamental difference between these two experiments appears to lie in the fact that in the former case the synthetic thyroprotein was fed as a constant

percentage of the ration from weaning onwards so that the actual intake of thyroprotein per pound body weight continuously declined as the pigs grew. In the latter case, on the other hand, the thyroprotein was fed as a constant dose per unit of body weight. This suggests that stimulation of growth rate may be obtained if small doses of thyroproteins are fed when the pigs are young and their metabolic rate is high, and if the intake of thyroprotein is decreased as body weight increases. Another feature which must be taken into account in interpreting the effects of experimentally induced hyperthyroidism is that thyroid administration, by increasing metabolic rate, may increase the requirement of various food factors such as the vitamins. Thus KORENCHEVSKY, HALL and CLAPHAM (1943) showed that the adverse effects of hyperthyroidism could be relieved to some extent by vitamin therapy and that relatively mild hyperthyroidism could be toxic if the ration was deficient in vitamins. This indicates that the increased metabolism in hyperthyroidism increases vitamin requirements.

Adrenal cortex

The cortex of the adrenal gland produces about 20 steroid hormones similar in structure to sex hormones and collectively known as cortin. Lack of cortin produces profound hypoglycaemia, loss of sodium chloride and water, retention of potassium, low blood pressure, weak heart action, reduced basal metabolism, disturbed temperature regulation and general muscular weakness. It is obvious that a gland so closely concerned with regulation of salt-water balance and with carbohydrate and protein metabolism will have a profound effect on growth.

As with thyroxine, administration of cortin to intact animals may have deleterious effects. As the body weight approaches maturity there is a sudden increase in the weight of the adrenal cortex, and it has been suggested by TURNER that increased adrenocortical activity may be responsible for bringing growth to a standstill.

Anterior Pituitary

The pituitary gland is the most important of the growth regulators. It is not essential in early embryonic life (FUGO, 1940) or in lower forms such as amphibia, but it is indispensable in mammals. It produces a series of trophic hormones which control the activity of other endocrine glands and hypophysectomy leads to atrophy of these, *e.g.* thyroids, adrenals and Islets of Langerhans. It follows from this that hypofunction of the pituitary upsets the whole metabolic process, which in turn has an adverse effect on growth. There is an extensive literature in human medicine on the effect of hypofunction and hyperfunction of the pituitary in man. Hypofunction results in

dwarfism and hyperfunction results in gigantism or acromegaly according to whether the hyperfunction occurs before or after the ossification of the epiphyseal cartilages. It was shown experimentally by CUSHING (1912) that removal of the anterior pituitary results in a cessation of growth. EVANS and LONG (1921) showed that growth was resumed in hypophysectomized rats if they were injected with anterior pituitary extract, and SMITH (1923) showed that the same result could be achieved by implanting pituitary tissue into hypophysectomized rats. Injections of anterior pituitary extract into young normal rats resulted in accelerated growth, and in the first experiments carried out by Evans and Long with female rats injected with anterior pituitary extract daily for 8 to 13 months, growth was continuous throughout the experiment but less rapid towards the end. In later experiments it was found that the rats made rapid growth during the early stages but later became refractory, growth ceased and in some cases they even lost weight. It soon became apparent that the injected animals were responding to the injections by producing 'anti-hormones' which were nullifying the effect of the injected hormones. This phenomenon has since been observed in connection with injections of other hormone preparations.

In the case of hypophysectomized rats there was a further reason for failure to respond indefinitely to injections of growth hormone in that hypophysectomy not only eliminates the growth hormone but also the trophic hormones which regulate the thyroid and adrenal cortex. Consequently, these glands regress and their secretions are insufficient to meet the demands occasioned by increased growth in response to the growth hormone. Thus it has been shown by EVANS *et al* (1935) that growth can often be elicited in hypophysectomized animals by injecting unpurified anterior pituitary extracts after purified extracts of growth hormone have failed to produce any further response. The reason for this appears to be that failure of the purified extract to produce any further growth is due to thyroid and adreno-cortical insufficiency. The unpurified extracts of the growth hormone contain traces of thyrotrophic and adrenocorticotropic hormones which stimulate the thyroid and adrenal cortex to increased secretion which in turn allows growth to proceed.

Since growth is always accompanied by an increase in body protein it has been suggested that growth promoting extracts of the anterior pituitary produce their effect by acting on protein metabolism. It has been shown that injection of anterior pituitary extract into dogs is followed by a fall in blood, non-protein nitrogen, urea and amino acids, by as much as 20–30 per cent (TEEL and WATKINS, 1929). There is also a reduction in excretion of nitrogen in the urine (GAEBLER, 1933). If the change in the composition of animals, in which growth has been accelerated by injections of anterior pituitary

extract, is determined chemically it can be shown that there is an increase in the proportion of water and protein and a decrease in the proportion of fats. This suggests that the effect of the growth hormone is to increase the rate of protein synthesis or to decrease the rate of protein catabolism. When injections of anterior pituitary extract are stopped, after a short period the weight gained is nearly all lost again. If, however, the injections are continued for longer periods, successively smaller proportions of the gain in weight are lost when the injections are stopped (LEE, 1936). This suggests that the first effect of the growth hormone is to increase the synthesis of labile proteins which are subsequently converted into less labile forms. It has been shown that the liver, in response to injections of anterior pituitary extract, increases in size to an extent disproportionately large in relation to the increase in body weight. Also changes in nitrogenous constituents are more striking in the liver than elsewhere. It is therefore suggested that anterior pituitary extracts produce increased protein synthesis in the liver, and MIRSKY (1939) has shown that nitrogen retention does not occur in response to injections of anterior pituitary extracts into animals from which the liver has been removed.

(4) VITAMINS

Until recently there has been little or no evidence of an effect on growth rate of a sub-clinical vitamin deficiency; that is, a state of vitamin deficiency which, while not sufficiently severe as to produce a characteristic disease, is sufficient to retard growth rate. It has long been known, however, that in the case of pigs and poultry, diets composed entirely of foods of vegetable origin were inadequate for producing maximum growth rate even though supplemented with all the known vitamins. When these diets were supplemented with animal protein foods, growth rates were greatly improved and this was ascribed to the presence in the animal product of an unidentified factor which came to be known as the Animal Protein Factor or A.P.F.

In 1948 RICKES and his co-workers and SMITH and PARKER independently isolated from crude liver extracts a vitamin, B_{12} , which is a specific factor in the treatment of pernicious anaemia. It was then found that vitamin B_{12} greatly improved the growth rate of chicks and pigs fed on wholly vegetable diets (OTT, RICKES and WOOD, 1948; HOGAN and ANDERSON, 1949). Thus vitamin B_{12} is concerned not only with haematopoiesis but also with the metabolism of proteins.

Vitamin B_{12} is apparently synthesized exclusively by micro-organisms so that while it is probably needed for normal growth in

all the higher animals the need for it is difficult to demonstrate in ruminants because of active microbial synthesis in the rumen.

It has been reported that vitamin B_{12} when given with all the other known vitamins is not fully as effective as animal protein food in maintaining growth rate in chicks and turkeys (SUNDE *et al*, 1950; HILL and BRANION, 1950). This indicates that there may be other, still unidentified, factors present in animal protein foods, but in addition it has been shown by COATES, HARRISON and KON (1950) that vitamin B_{12} could replace animal protein food in chicks from normal hens, but not if the hens had previously been maintained for some months on a diet deficient in vitamin B_{12} .

(5) ANTIBIOTICS

Although vitamin B_{12} was originally isolated from crude liver extract it is produced by microbiological activity and it is now manufactured by a fermentation process similar to that used in the manufacture of antibiotics. STOKSTAD *et al* (1949) supplemented all-vegetable ration for chicks with a fermentation product, *streptomyces aureofaciens* mash, as a source of vitamin B_{12} and found that a much better growth rate was obtained than by supplementing with vitamin B_{12} alone or with vitamin B_{12} plus animal protein factor. STOKSTAD and JUKES (1950) showed that a growth response was produced in chicks on a vegetable diet by the addition of crystalline aureomycin hydrochloride and in 1951 they showed that the growth stimulating effect of aureomycin was produced in the presence or absence of vitamin B_{12} .

The pioneer experiments of Stokstad and Jukes have been followed by a very large number of experiments on the effects on growth rate of feeding various antibiotics to different farm animals. The antibiotics commonly used are penicillin, aureomycin, streptomycin, terramycin, chloromycetin and bacitracin. In all cases antibiotics improve the growth rate of pigs and poultry on an all-vegetable diet, but the response of animals on diets containing animal protein supplements is less certain and appears to depend to some extent on the conditions under which the animals are kept. For example, DAVIS and BRIGGS (1950) found that the growth rate of chicks without antibiotics in their diet but reared in new houses was as good as the growth rate of chicks receiving antibiotics but reared in old houses. In another case (COATES *et al.*, 1951) it was found in one laboratory that penicillin had no effect on the growth rate of chicks which were given animal protein but in a similar experiment in another laboratory penicillin had a beneficial effect. A joint experiment in which chicks of the same batch were divided between the two laboratories and were given the same food, produced the same result as before, *i.e.* a response to penicillin at one place but not at the other. The

only difference between the two groups was that in the case of the chicks where a response to penicillin was obtained the houses had been previously used for poultry, but where there was no response the houses had not previously been used for poultry. It was concluded that the difference in response to penicillin was due to an unsuspected infection in the chicks in the houses previously used for poultry. A comparison was made by LUCKEY (1952) between the growth response to various antibiotics fed to normal and germ-free chicks and it was found that whereas normal chicks responded to antibiotics the germ-free chicks did not. It was therefore concluded that antibiotics produce their effect by their action on the microflora of the gut. In confirmation of this it is found that a growth response to antibiotics is only produced by oral administration and not by injection.

There is some evidence that the accelerated growth response to feeding antibiotics is dependent on a continuous intake of the antibiotic. Thus BERG *et al.* (1950) found that an accelerated growth rate in chicks resulted from the use of an aureomycin fermentation product during the first $4\frac{1}{2}$ weeks of life. The accelerated growth response ceased when the antibiotic was discontinued at this stage but chicks which were given the antibiotics for the first time at this age showed the accelerated growth response indicating that it is dependent on a continuous intake of antibiotic.

In the case of pigs the growth response is similar to that recorded in chicks in that it is greater in the case of pigs kept under rather insanitary conditions, and SPEER *et al.* (1950) found that antibiotics were ineffective if given to pigs under very good hygienic conditions. Where a response to antibiotics is obtained with pigs it is greatest in the case of pigs between weaning and about 100 lb live weight.

In the case of cattle MACKAY, RIDDELL and FITZSIMMONS (1953) found a significant increase in growth rate and improved appetite and appearance in young calves up to 12 weeks of age receiving a liberal supply of milk, calf starter and good quality hay plus terramycin. There was no improvement in food conversion rate and it was concluded that the beneficial effect of terramycin was due to increased appetite.

The exact mode of action of antibiotics in stimulating growth rate has not yet been fully worked out but it seems clear that the effect is produced through their influence on the microflora of the gut. The fact that growth stimulation is greatest in unthrifty animals and in animals kept in unhygienic surroundings suggests that one effect of antibiotics is to combat actively pathogenic organisms which, while not actually producing clinical signs of disease, are producing toxins which have a growth depressant effect. In addition to this, however, the fact that a response is frequently obtained with pigs kept under quite good conditions suggests that antibiotics may alter the

composition of the microflora of the gut in such a way as to reduce the number of certain micro-organisms which, while not actively pathogenic, may depress growth rate by competing with the host for nutrients. Furthermore, it is possible that there are still unrecognized vitamins which are necessary for growth and it may be that in some cases the effect of the antibiotics is to favour the growth of micro-organisms producing these vitamins by eliminating competition from other non-beneficial micro-organisms.

AGING AND SENESCENCE

The problems of aging and senescence have attracted a good deal of attention in human physiology but very little in the physiology of the domestic animals. Animals which are slaughtered for meat are still physiologically immature at slaughter; for example, the pig is normally slaughtered when it is six or seven months old but it would not be mature until it is four or five years old and its possible life span would be much longer, possibly ten or fifteen years. It, therefore, follows that, even if conditions under which pigs are fattened in normal farm practice would ultimately lead to early senescence and shorten the life span from, say, ten to eight years, this is of no practical consequence if the animal is slaughtered when it is six months old.

Problems of aging and senescence can only be important in the case of breeding stock where lifetime performance is a major consideration. In breeding stock deaths from old age are rare and any connection between premature senescence and the reasons for breeding stock having to be slaughtered is not very obvious if it exists at all. The most frequent reasons for slaughter of breeding stock are reproductive failures, low productivity and disease.

Little or no research has been carried out with farm animals on the relationship, if any, between senescence and these reasons for disposal of breeding stock, but in view of the high rate of wastage in farm breeding stock it would appear that the relationship between, for example, growth rates and the above reasons for disposal of breeding stock would repay investigation.

Much of the present knowledge of the problems associated with aging and senescence is derived from human medicine and most of the experimental work has been carried out with unicellular organisms, with tissue cultures and with small laboratory animals.

In the case of humans it has been shown that age at death is determined by two main causes:—

- (1) External, including accidents and infections.
- (2) Internal, including slowly developing degenerative diseases.

These two causes are interrelated to some extent, for example, accidents to old people are more likely to be fatal because of reduced resistance, brought about by internal degenerative changes. In so

far as medical science has been successful in prolonging human life it has done so mainly by reducing the death rate from external causes. Evidence of this is provided by the decrease over a period of years in the proportion of deaths caused by diseases such as tuberculosis and an increase in the proportion of deaths caused by cancer.

Senescence and death are not inherent in unicellular organisms which will divide continuously providing they are supplied with food and providing the waste products of metabolism are not allowed to accumulate. If, however, the food supply becomes exhausted or if the products of metabolism are not removed growth stops, senescence sets in and death follows.

Similarly tissues of higher animals are capable of living and growing indefinitely as was shown by Loeb (1908) who grew cancer tissue continuously by transplanting it to successive generations of animals. Carrell (1933) showed that normal tissues could be kept alive indefinitely in tissue culture. Thus while cells can be kept alive indefinitely under suitable culture conditions, when they form part of the closed system represented by the animal body they ultimately age and die. DHAR (1930) propounded a physico-chemical theory of aging based on analogy with aging in non-living colloids. He pointed out that many changes which occur with age in the body are analogous to the changes which occur when non-living colloids are setting, *i.e.* progressive dehydration, reduction in elasticity, surface energy and chemical reactivity.

On this theory any factor which accelerates metabolic rate increases the rate of aging. Such factors are muscular work, overfeeding, overactive nervous and endocrine systems and environmental temperature.

Overfeeding has been shown to shorten the life span (McCAY *et al.*, 1941); unfavourable factors arising from overfeeding are increased metabolic rate and mechanical obstruction of organs and muscles with fat. HESS (1933) suggested that diabetes could result from overfeeding. Overfeeding caused hypertrophy of the Islets of Langerhans, which in turn produced an excess of insulin and this insulin led to an increased appetite, thus setting up a vicious cycle. Ultimately the hypertrophy of the islets was followed by degeneration and diabetes.

Excess vitamin intake does not appear to have a deleterious effect except possibly in the case of vitamins A and D and even in these cases there is no danger if the vitamins are administered in natural foods. The requirements for vitamins tend to decline with age but vitamin intake should actually increase with age to compensate for reduced absorption (IRVING and RICHARDS, 1939).

As overfeeding increases the rate of senescence and shortens the life span, so underfeeding, particularly restriction of calorie intake,

LIVE-WEIGHT GROWTH

increases the life span. Thus in the series of experiments carried out by McCay and his co-workers (McCay *et al.*, 1939) in which groups of rats were kept on a restricted caloric intake for periods up to 1,000 days, it was found that some members of each of the retarded groups were alive after the last of the controls had died. While it is impossible to say how long the survivors might have lived if their diet had not been restricted, nevertheless the fact that none of the control rats lived to a comparable age is strong evidence that the restricted caloric intake prolonged the life span. The effect of the restricted energy intake was to slow down the growth rate and to delay the attainment of maturity after which the degenerative changes associated with senescence normally set in. In other words the restricted caloric intake delayed the onset of senescence by prolonging the juvenile period. These rats were kept in a protected environment, *i.e.* temperature controlled and air conditioned, and it is not clear that the prolongation of the life span would have been so effective if the rats had been exposed to the normal incidence of infections and similar hazards. Thus, although the restricted food intake postponed the slow degenerative changes associated with senescence it is possible that resistance to infections might have been reduced.

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CHAPTER 10

CONFORMATION AND BODY COMPOSITION

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A STUDY of the way in which the adult shape of the animal is developed and of the factors which influence the composition of the body is important, for the value of our meat animals depends on these changes. While the general anatomy of our farm animals is well known, the physiology of the means by which the various forms of animals are produced and how various environmental and other factors affect them, was comparatively unknown until recently. Medical science has studied the effects of exercise and stresses on the shape of various muscles and bones, but this plays only a small part in natural development although it may come into play as a result of accidents. The producer of farm animals requires to be able to control the shape of his animals, but before this can be done we require to know what are the physiological factors concerned.

CHANGES WITH AGE

GENERAL PRINCIPLES AND METHODS OF MEASURING DEVELOPMENTAL CHANGES

During the process of growth all organisms save the simplest not only increase in size but also undergo changes in form due to differential growth rates of their constituent parts (THOMPSON, 1917, 1942; HUXLEY, 1932; BRODY, 1945). In the animal kingdom the change in form or conformation from the fertilized ovum to the shape of the adult animal is more pronounced and goes on for a relatively longer period of the animal's life in the higher than in the lower forms, for example, in mammals as compared with fishes. HECHT (1916) found that in fishes the external form is established early in the post embryonic life of the individual and is adhered to within rather narrow limits for the rest of its life. He noted that this occurred only in vertebrates with indeterminate growth, *i.e.* with no fixed limit of adult size, whereas in mammals having determinate growth, the external form changes continually during the period of growth, and as soon as the form becomes constant, growth ceases (*Figures 10.1 and 10.2*). He concluded that this early constancy of form in fishes is an adaptation to aquatic life.

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HAMMOND (1952a) defines *growth* and *development* as follows: 'As an animal grows up two things happen: (1) It increases in weight until

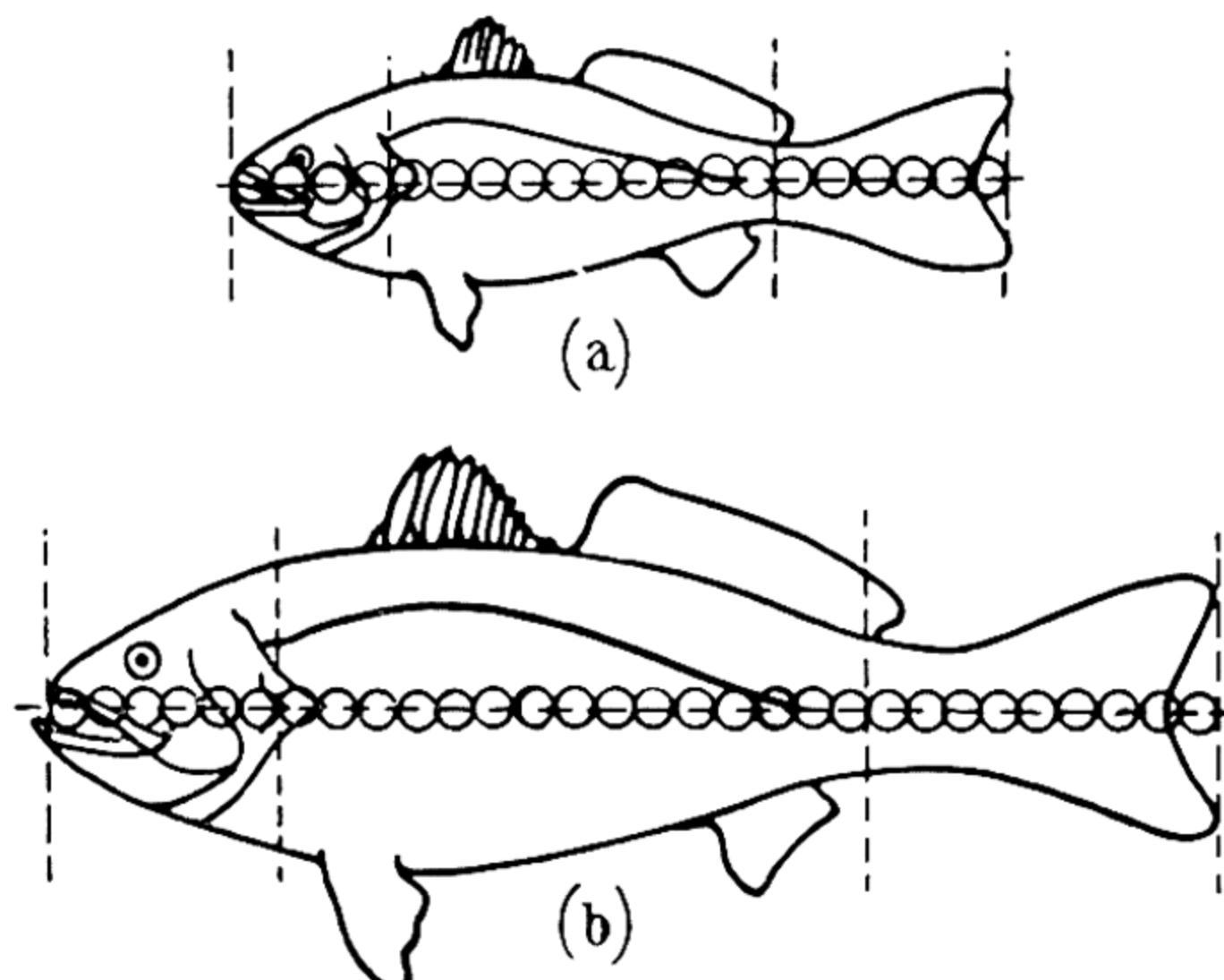


Figure 10.1. Showing the similarity of external form and proportions in a small fish (a) and a large fish (b). The small circles indicate a linear enlargement of one-half in the length of the body and parts of the larger fish. (From Hecht, 1916, by courtesy of *J. Morph.*)

mature size is reached; this we shall call *Growth*, and (2) it changes in its body conformation and shape, and its various functions and faculties come into full being; this we shall call *Development*'.

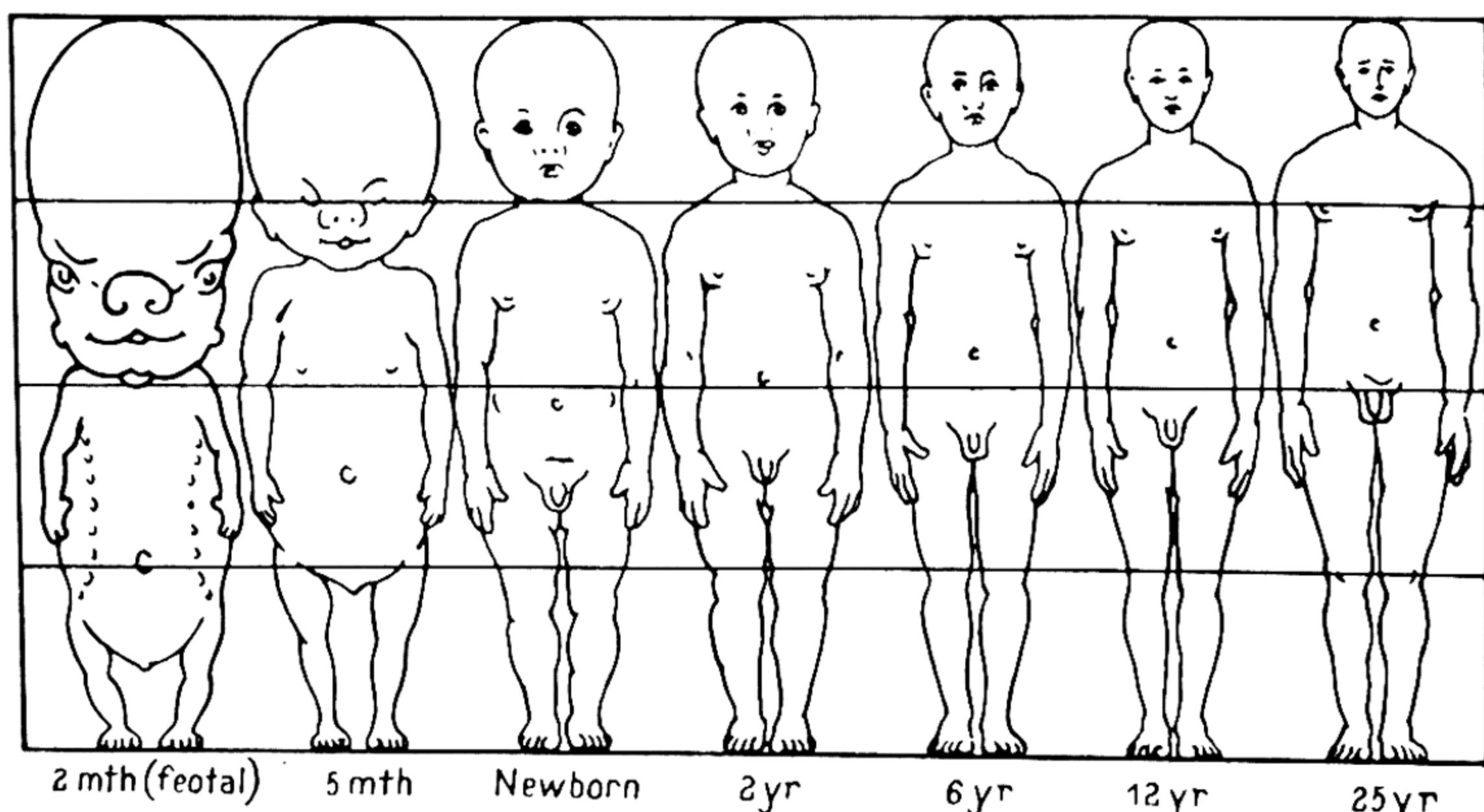


Figure 10.2. Illustrating changes in form and proportions of the human body during foetal and postnatal life. (From Robbins *et al*, 1928, after Stratz, by courtesy of Yale University Press.)

There are many ways of measuring growth, as the actual weight or growth curve, the percentage increment method, and the weight gained per fixed unit of time (MINOT, 1907; BRODY, 1921, 1926, 1927, 1945; HUXLEY, 1932; HAMMOND, 1932a, 1952a; ZUCKERMAN *et al*, 1950). The method used depends mainly on the point of view from

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which growth has been studied. Workers who are primarily interested in practical application of growth studies usually either use the actual increment per unit of time or the actual growth curve, whereas those studying theories of growth have generally used the percentage increment method (Minot, 1907). Thompson (1917) maintains that the increment per unit of time method in measuring growth rate shows up differences better than the percentage increment method.

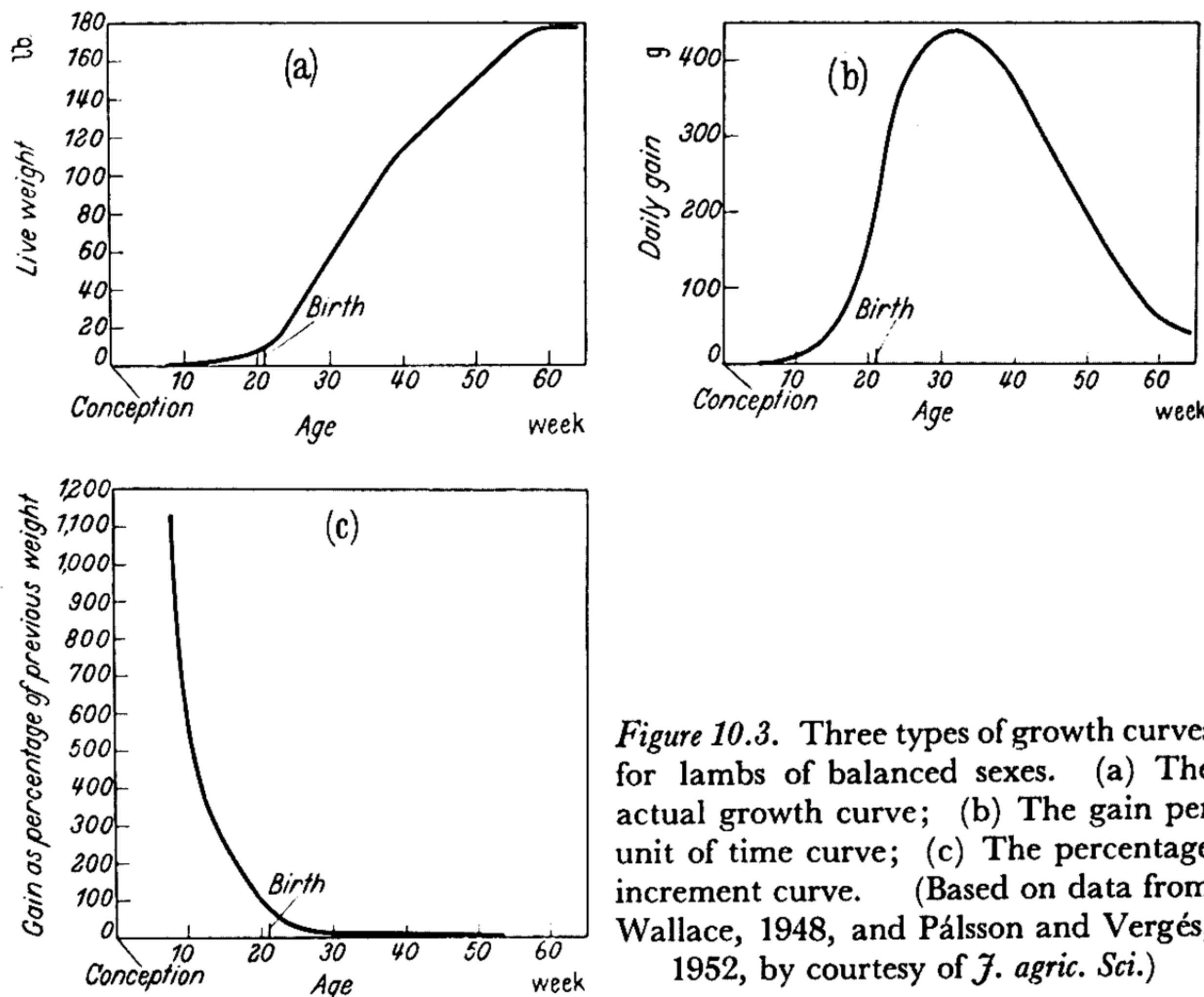


Figure 10.3. Three types of growth curves for lambs of balanced sexes. (a) The actual growth curve; (b) The gain per unit of time curve; (c) The percentage increment curve. (Based on data from Wallace, 1948, and Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

These three methods of measuring growth give fundamentally different pictures graphically (*Figure 10.3*). The actual growth curve, live weight plotted against age, has an 'S bend shape' (*Figure 10.3a*) and is very similar in shape for all farm animals as well as for laboratory animals (Brody, 1927), whereas in man it is very different due to the prolonged infantile and juvenile period (*Figure 9.1*). KAUFMAN (1929) has found that post-hatching growth curves for chickens and pigeons differ greatly in form due to the much slower rate of growth of the former during the first weeks after hatching (*Figure 9.4*). The actual gain per unit of time is always slow at first, then increases to a maximum and slows down somewhat more gradually again, giving a curve of the type illustrated in *Figure 10.3b*, whereas the increment as a percentage of the previous weight of the individual is always great at first, falling rapidly as the weight of the animal increases (*Figure 10.3c*), thus giving a curve opposite in shape to the actual growth curve.

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Developmental changes can also be measured and demonstrated in various ways. They can be estimated either by body or carcass measurements or by weight of different organs, parts or tissues of the body. Numerous workers studying growth and development of animals have used the external body measurements technique extensively. Any changes in body conformation, which are estimated

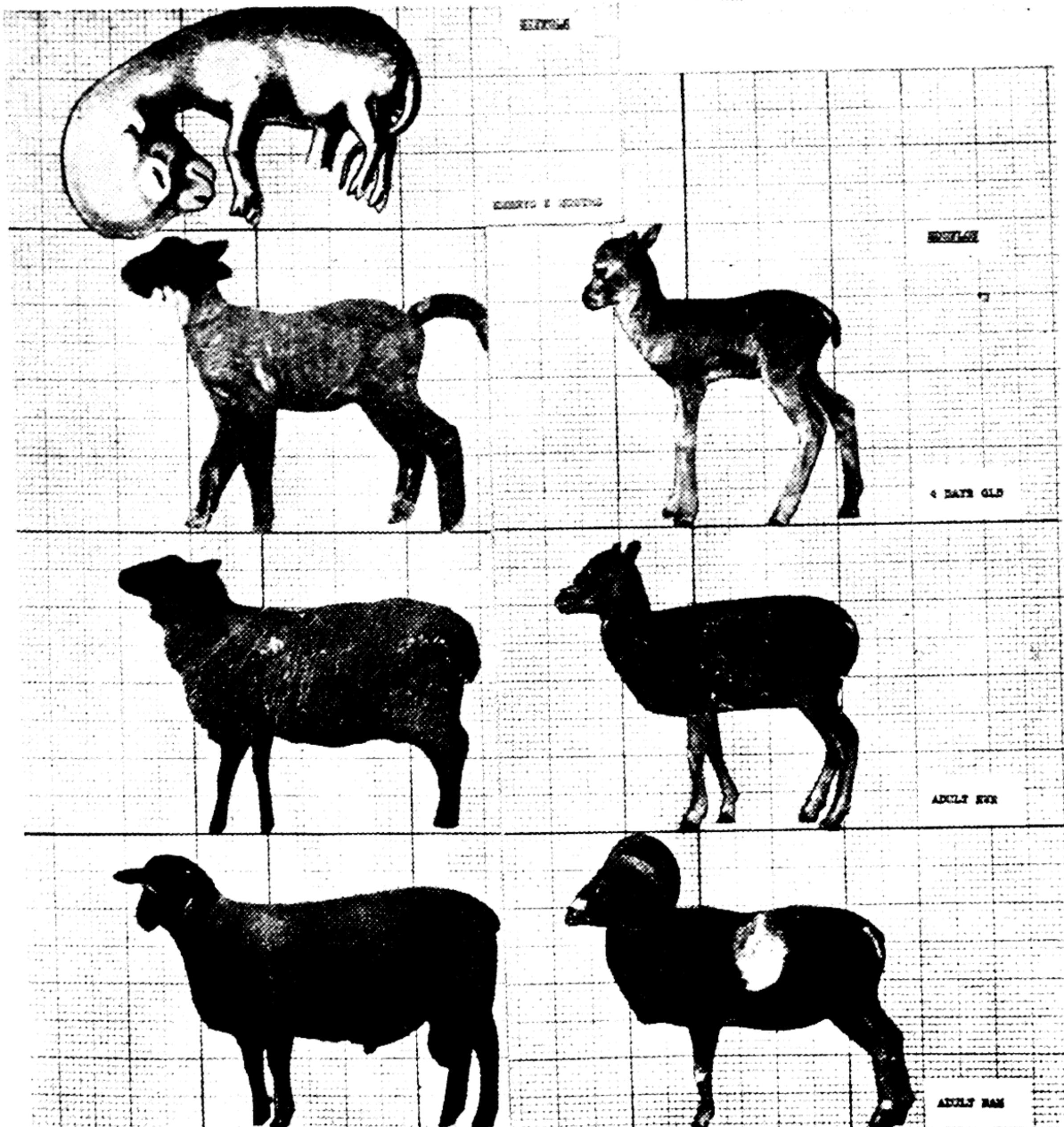


Figure 10.4. Changes in the proportions of the improved Suffolk (*left*) and the unimproved Mouflon (*right*) breeds of sheep as they grow up. Each is reduced to the same shoulder height so as to show differences in proportions as distinct from differences in actual size. *Top*—Embryo at 2 months. *2nd line*—4 days old. *3rd line*—Adult ewe. *Bottom*—Adult ram. (From Hammond, 1932a, by courtesy of Oliver and Boyd.)

by external body measurements, can best be demonstrated by expressing the various measurements at any one age as percentages of the same measurement at another age. The measurements at different ages can also be expressed as a percentage of some standard

measurement at the same age. The standard measurement is preferably that of an early maturing character such as height at withers or length of cranium, thus indicating the relative differences in the rate of change in the various body measurements with age. Actual linear changes in body conformation are often most clearly demonstrated photographically by keeping one measurement of an early maturing character, such as height at withers or cranium length, constant in all the photographs so that any developmental changes can easily be distinguished from changes in size (*Figure 10.4*; Hammond, 1932a). External body measurements are primarily indices of length growth of skeletal parts (Hammond, 1932a) and therefore though useful to elucidate general trends in changes in conformation of an animal with age they do not give any information as to the changes in weight or composition of the different parts of the animal's body. These latter are of much greater interest both to the producer and consumer of meat and to the scientist, whether he be a nutritional or growth specialist or both.

Hammond (1932a) in his work on the growth and development of mutton qualities in the sheep developed a new technique for the study of growth and developmental changes in animals. This is not only useful from a scientific point of view but is also of particular importance in the practical application of growth studies to problems of meat production. This is the complete dissection method, *i.e.* the total body is separated anatomically into its component organs, parts and tissues and the weight of each recorded; measurements are also taken of individual bones of the skeleton. Hammond's dissection technique has since been used by several members of his school (McMEEKAN, 1940, 1941; PÁLSSON, 1939, 1940; WALLACE, 1948; and PÁLSSON AND VERGÉS, 1952). Hammond (1932a) describes four methods by which developmental changes may be measured when data are available on actual weights of the various organs, parts or tissues of the body. The first method is to show the organ, part or tissue as a percentage of the whole, *i.e.* as a percentage of the total body weight, or the weight of one organ as a percentage of the total weight of all organs, etc. This method is important from the practical point of view, while in growth studies it has a serious disadvantage in that the proportions of one organ, part or tissue are affected by changes in others, so it is often not clear whether one organ or part is abnormally large or other organs or parts are abnormally small. In a rapidly fattening animal, for example, the weight of muscle as a percentage of live weight or carcass weight may be decreasing even though the actual weight of muscle is at the same time increasing.

The second method is to compare organs or parts with a standard organ or part; the result is then not affected by growth of other organs or parts. It is important, however, that the standard organ

or part be carefully selected as one not liable to great fluctuations in size; for this reason it should be preferably an early maturing one such as the brain, the eye-balls or the cannon bones. Large fluctuations in the standard organ or part will cause great disturbances in the curves.

The third method is to compare the weight of organs, parts or tissues at different ages with the weight of the same organs, parts or tissues at a constant age, for example at birth. This is a suitable method by which to study age changes.

The fourth method is the rate of gain in weight of an organ or part per fixed unit of time. Unfortunately, when dissections of animals have to be performed the time intervals between dissections are usually too long to give accurate results of the growth rates of the different organs or parts. This method is therefore more easily applicable when external body measurements are used, as they can be recorded at regular and relatively short intervals of time.

A fifth method, suitable when effects of environmental factors such as the plane of nutrition on developmental changes are studied, is to express the weight of organs, parts or tissues of different treatment groups at any age as a percentage of the weight of the same organs, parts or tissues of one of the treatment groups at the same age. Any differences in the degree of development of the treatment groups are shown up best by selecting as a standard group the one which is least advanced in development (McMeekan, 1940, 1941; Pálsson and Vergés, 1952).

Numerous early workers (GLÄTTLI, 1894; NATHUSIUS, 1905; MEEK, 1901; WATERS, 1908, 1909; LOWREY, 1911; ECKLES and SWETT, 1918; BRODY and RAGSDALE, 1924; HANSEN, 1925; HERING, 1925; REIMERS, 1925, 1927; LUSH, 1928; SCHMIDT and LAUPRECHT, 1928; ISAACHSEN, 1933; Hammond, 1932a) engaged in growth studies in farm animals, using external body measurements and live weight changes as a criterion on which to base their judgment, found that during the postnatal stage of growth live weight increased at a much faster rate than any body measurement. Measurements of the skull followed by that of the height at the croup or at the withers increased at a much slower rate than the measurements affected to some extent by muscles or fat development, such as the circumference and width of heart girth. They also found that measurements of length and thickness growth of the hindquarters, such as the length and width of the pelvis, had a higher rate of growth in postnatal life than those of the head and the forequarters (*see* pages 447-449). From this evidence these writers concluded that at birth the skeleton was relatively much better developed than the flesh which makes up the greatest proportion of the weight in the full grown animal. Furthermore the head, the limbs and the forequarters were relatively

better developed at birth than the hindquarters, and that in postnatal life a gradient of increasing growth rate passed from the head backwards to the pelvic region. Consequently, growth in prenatal life was characterized by a relatively high rate of growth in the head and the limbs.

Hammond (1932a), using data from completely dissected animals for a comparative study of the development of sheep at different ages from birth to maturity (4 years), not only confirmed the findings of previous workers that different parts of the animal's body grow at different rates in postnatal life, but in addition he elucidated and outlined in detail the fundamental principles underlying developmental changes in different anatomical regions, and in the major tissues and organs of the body, which added together account for the changes in the conformation of the animal from birth to maturity. Later, other workers using Hammond's techniques (McMeekan, 1940, 1941, in the pig; VERGÉS, 1939a, b; Pálsson and Vergés, 1952, and Wallace, 1948, in the sheep) and using larger numbers of animals kept under complete experimental control added further proof to and extended in greater detail Hammond's theory of differential or heterogonic growth in farm animals from the foetal stage to mature weights. The same general principles of growth and developmental changes apply in the two widely different species, the sheep and the pig; slight species differences occur, however, due to the fact that the pig is born much more immature than the lamb and is therefore at birth both physiologically and anatomically younger than the lamb. In brief, the findings of these workers show that the developmental changes in the animal are caused by a primary wave of growth from the cranium down to the facial parts of the head and backwards to the lumbar region. A secondary wave of growth starts from the lower parts of the limbs (metacarpals and metatarsals) down to the digits and upwards along the limbs and the trunk to the lumbar region, which is the last part of the body to attain its maximum growth rate and is consequently the latest maturing part of the animal. A similar pattern of an early onset of high growth intensity at centres near the extremities passing with an increasing growth rate backwards and upwards to the lumbar region is also met with in each of the major tissues, bone, muscle and fat. Bone growth in length takes place earlier than growth in thickness. The different tissues also attain their maximum rate of growth in a definite order with age as follows, (1) nervous tissue, (2) bone, (3) muscle, and (4) fat. Moreover, fat is accumulated in the various fat depots with age at different rates in the following order of increasing rate: mesenteric fat, kidney fat, intermuscular fat, and subcutaneous fat. The different organs and organ groups also exhibit marked heterogonic growth; some, like the eyes, with a very early onset of high growth rate, being the best developed organs at

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birth. The kidneys and the heart are also early maturing though attaining their maximum gain per unit of time later than the eyes. The thoracic organs as a whole are earlier maturing than the digestive tract. Whether an animal is early or late maturing depends on the time it takes the individual to pass through these developmental changes described above (Hammond, 1932a). *Figure 10.5* illustrates diagrammatically how the different parts and tissues of the body attain their maximum rate of growth at different ages for an early maturing and a late maturing animal respectively. *Figure 10.4* illustrates photographically the developmental changes in the body proportions from 2 months after conception to maturity in the early

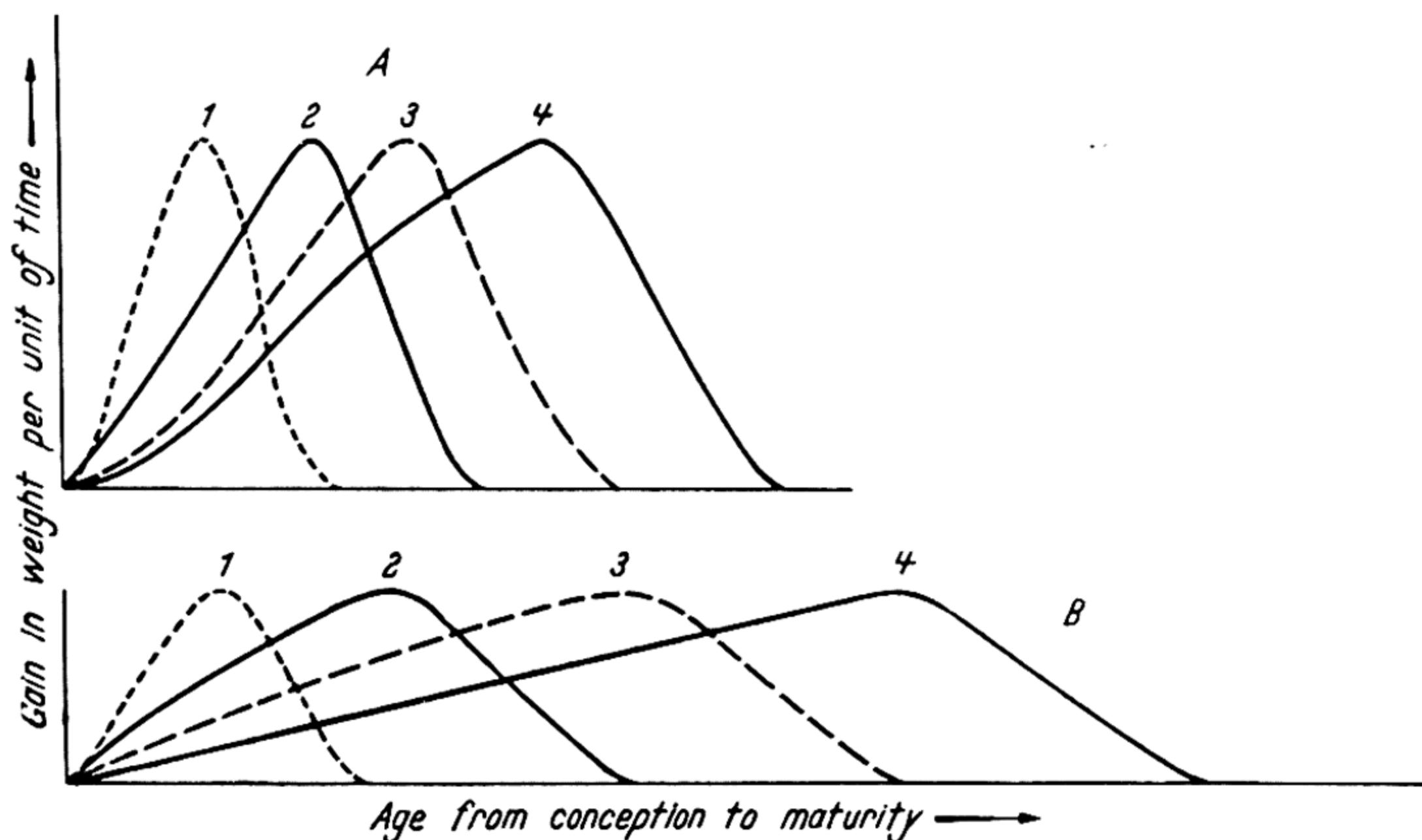


Figure 10.5. The rate of increase in weight, showing the order of development of the different parts and tissues of the body and the way in which the changes in shape and body proportions are affected by early and late maturity and/or the level of nutrition.

A = early maturity or high plane of nutrition.

B = late maturity or low plane of nutrition.

Curves: 1	2	3	4
Head	Neck	Thorax	Loin
Brain	Bone	Muscle	Fat
Cannon	Tibia-fibula	Femur	Pelvis
Kidney fat	Intermuscular fat	Subcutaneous fat	Marbling fat

maturing Suffolk sheep and from birth to maturity in the primitive late maturing Mouflon sheep. At 2 months of foetal life the head, particularly the cranium, is proportionately very large due to the early onset of high growth intensity of the brain, eyes and skull, while the limbs are at that stage still relatively short. At birth both head and feet make up a relatively large proportion of the whole body while the trunk is short, shallow and narrow. In postnatal life the body increases in length, depth and width in that order due to the heterogonic growth of its constituent tissues and parts described above.

In both breeds as adults the ram has better developed body proportions than the ewe. A striking difference between the breeds is obvious. The newborn lamb of the early maturing breed has nearly as well developed body proportions as the adult ewe of the late maturing primitive breed, while the mature ewe of the former breed has better developed proportions than the mature ram of the latter. A low plane of nutrition during the growing period of the animal's life lengthens the time needed for the animal to pass through the developmental changes. The result of this is that an early maturing animal reared on a low plane of nutrition during growth takes on the form of a late maturing one (McMeekan, 1940, 1941; Pálsson and Vergés, 1952, *see below*, pages 475, 501).

SIZE AND BODY PROPORTIONS AT BIRTH

In order to appreciate the factors which affect the proportions of the body at birth it will be necessary first to consider size at birth, for within a species body size affects body proportions. For growth studies it is necessary to distinguish between the chronological age of an individual and its physiological age (Brody, 1945). The chronological time is measured by the rotations of the earth around its axis and is assumed to flow uniformly while physiological time is measured by the rate of change in the organism and is therefore variable. Quoting Brody (1945): 'If the life span is 90 days in *Drosophila* and 90 years in *Homo*, we may say that the physiologic clock of the fly runs about 365 times as rapidly as that of man'. There is a great species difference in the physiological age of the young at birth mainly depending on how great a part of the growing period is spent *in utero*. The rabbit is born very immature or physiologically young (HAMMOND and MARSHALL, 1925) and similarly the rat (DONALDSON, 1915), whereas the guinea pig is born in a relatively mature state or physiologically much older (Minot, 1907).

Among farm animals, the foal is born in the most advanced state of development and is physiologically older than the young of other species; at birth it is about 9 per cent of its mature weight (Isaachsen, 1933). The lamb and the calf are born slightly younger physiologically, while the pig is by far the most immature of all farm animals at birth, its birth weight being less than 1 per cent of the mature weight of the species (Lowrey, 1911; McMEEKAN *et al.*, 1943). Within species, breed differences and other genetical factors affect birth weight. Several other factors such as the nutrition of the dam, sex, the number of young born, length of gestation, age and size of dam, have an influence on birth weight.

In multiparous animals, the weight at birth varies with the number born, members of large litters being smaller than those of small litters (KING, 1935).

In the rabbit, HAMMOND (1934) found that the average weight of individual young at birth varied from 44 g. in litters of thirteen to 98 g. in litters of one. As small litters, however, have usually longer duration of pregnancy than large ones, WISHART and HAMMOND (1933) calculated that the decrease in birth weight is from $1\frac{1}{2}$ to $2\frac{1}{2}$ g. per young for each additional individual in the litter independent of the decrease in weight due to the shortened length of pregnancy in large litters. It is, however, only in the later stages of pregnancy that large litters have an inhibiting effect on the growth rate of the individuals (IBSEN, 1928).

In the sheep, twins are as a rule born lighter than singles and triplets lighter than twins (Hammond, 1932a; Vergés, 1939a; McMEEKAN *et al*, 1943; FRASER, 1951; Wallace, 1948). Singles may be some 120 per cent and triplets 90 per cent of the weight of twins at birth (Hammond, 1932a). Nutrition of the dam during the latter half of pregnancy has a profound influence on the relative weight of singles, twins and triplets (Vergés, 1939a; WALLACE, 1944, *see* page 477).

In pigs, the numbers of pigs in a litter has a great influence on the average weight of the individuals (CARMICHAEL, 1916; SCHMIDT, 1924; HEMPEL, 1928; RODEWALD, 1928; OLOFSSON and LARSON, 1930; MCKENZIE, 1928; and LUSH *et al*, 1934). Hempel (1928) found in the German Hannover-Braunschweig Landschwein that the average weight per pig varied with the number in the litter as follows: In litters of ten or more the average weight per pig was 1.18 kg., in litters of from six to ten pigs, 1.38 kg.; and in litters of less than six pigs, 1.53 kg. Lush *et al* (1934) found that the heaviest pigs at birth were from litters of three to five pigs.

The age of dam also influences birth weight. In the sheep, PRAWOCHENSKI and KACZKOWSKI (1926), Hammond (1932a) and BONSMA (1939) all found that lambs from two-year-old ewes were significantly lighter than lambs from mature ewes. In cattle, FITCH *et al* (1924), ECKLES (1919, 1920), TYLER *et al* (1947) and VENGE (1948) have all found that calves of first calvers are lighter than those from mature cows. Tyler *et al* (1947) found that on the average this difference amounted to 10 lb. per calf. Eckles (1919, 1920) found that third to sixth calvers gave the heaviest calves at birth, while old cows gave calves slightly lighter than the average. In pigs, CARMICHAEL and RICE (1920) showed that young sows produce smaller litters with a smaller average weight per pig at birth than older sows. The reason why a young dam gives birth to smaller offspring is undoubtedly a nutritional one. The maternal tissues, not being as yet full grown, compete with the foetal tissues for available nutrients in the blood stream (*see* page 476).

The size of the dam has a great influence on the size of the young at birth. Not only do females of the larger breeds give birth to

larger offspring than those of the smaller breeds but so do large individuals within a breed. In sheep, HUMPHREY and KLEINHEINZ (1908), RUSSELL (1919), LAPLAND and DUFFAN (1923), Hammond (1932a), DONALD and MCLEAN (1935), and Bonsma (1939), and in cattle, Eckles (1919), KNAPP *et al* (1942), and Venge (1948) have found that large dams give birth to larger offspring than smaller dams; some of these authors found the size of the dam to be the most important single factor in determining birth weight.

The maternal influence due to size appears to suppress to a considerable extent the genetical influence of the male when cross-breeding is performed between breeds of different size. In an experiment with reciprocal crosses between the large Shire horse and the small Shetland pony, WALTON and HAMMOND (1938) found that the size of the foal follows the size of the dam. The mother, possibly through hormonal action, appears to be able to control the size of the offspring in spite of its genetical constitution, at least within certain limits. The crossbred foal out of the Shire mare is at birth three times as large as the crossbred foal out of the Shetland mare, each foal resembling more a pure-bred foal of the mother's breed than an intermediate (*Figure 9.8*). Though decreasing in postnatal life these differences did not disappear; at four years old the former was still one and a half times heavier than the latter. In rabbits, VENGE (1950) experimenting with reciprocal crosses between large and small breeds and also by fertilized ovum transplantation from a large to a small breed and *vice versa* has also found marked maternal effects in controlling the size of the young in spite of its genetical constitution. His results, however, do not show as great a maternal influence as observed in the Shire-Shetland crosses; this may be due to the fact that the rabbit is born physiologically much younger than the horse, *i.e.* intra-uterine maternal effects last for a relatively longer part of the growing period in the horse. HUNTER (1954), in sheep, made reciprocal crosses between the large Border Leicester and the small Welsh breed and compared these with lambs of both pure breeds. He found a slight maternal effect in the reciprocal crosses, the crossbred lambs from the large mother being somewhat heavier than those from the small mother. Comparison of the crossbred and the purebred lambs out of the large and the small mothers respectively showed that the small ram has less influence on the size of the lamb from the large dam than the large ram has on the lamb from the small dam.

The available evidence on this subject, though insufficient, is of great practical importance for the livestock breeder as it emphasizes the value in crossbreeding of using females of large breeds in order to obtain rapid development of the progeny while the use of a male of a smaller improved breed gives better carcass quality than the use of large males for that purpose.

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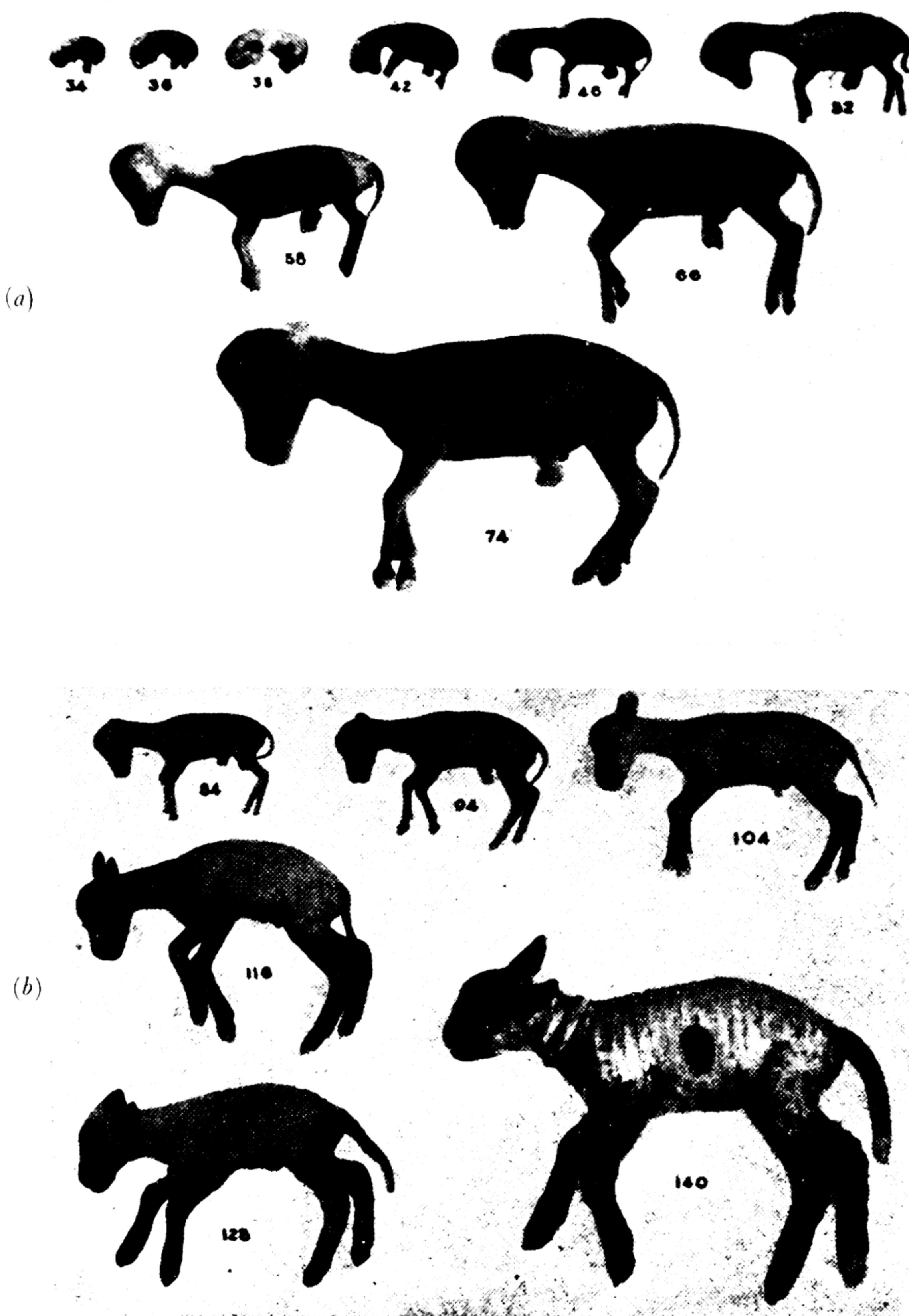


Figure 10.6. Foetal development in the sheep. The specimens in the top half (a) were all photographed at one magnification and those in the bottom half (b) are another magnification. The age in days is indicated by the numbers below each specimen. Note the proportionately very large cranium in the early stages followed by relatively great increase in length of the limbs and facial parts—the fore limbs grow for a while at a faster rate than the hind limbs while this is later reversed. During the last stages length and depth of body increase proportionately more than during the early stages. (From Winters and Feuffel, 1936, by courtesy of *Univ. Minn. Agric. Exp. Sta. Tech. Bull.*)

GROWTH

Within breeds birth weight is an indication of anatomical and physiological age as distinct from chronological age. This is of great practical importance in farm animals as the new born of less than the average weight for its breed, due to under-nutrition of the dam,

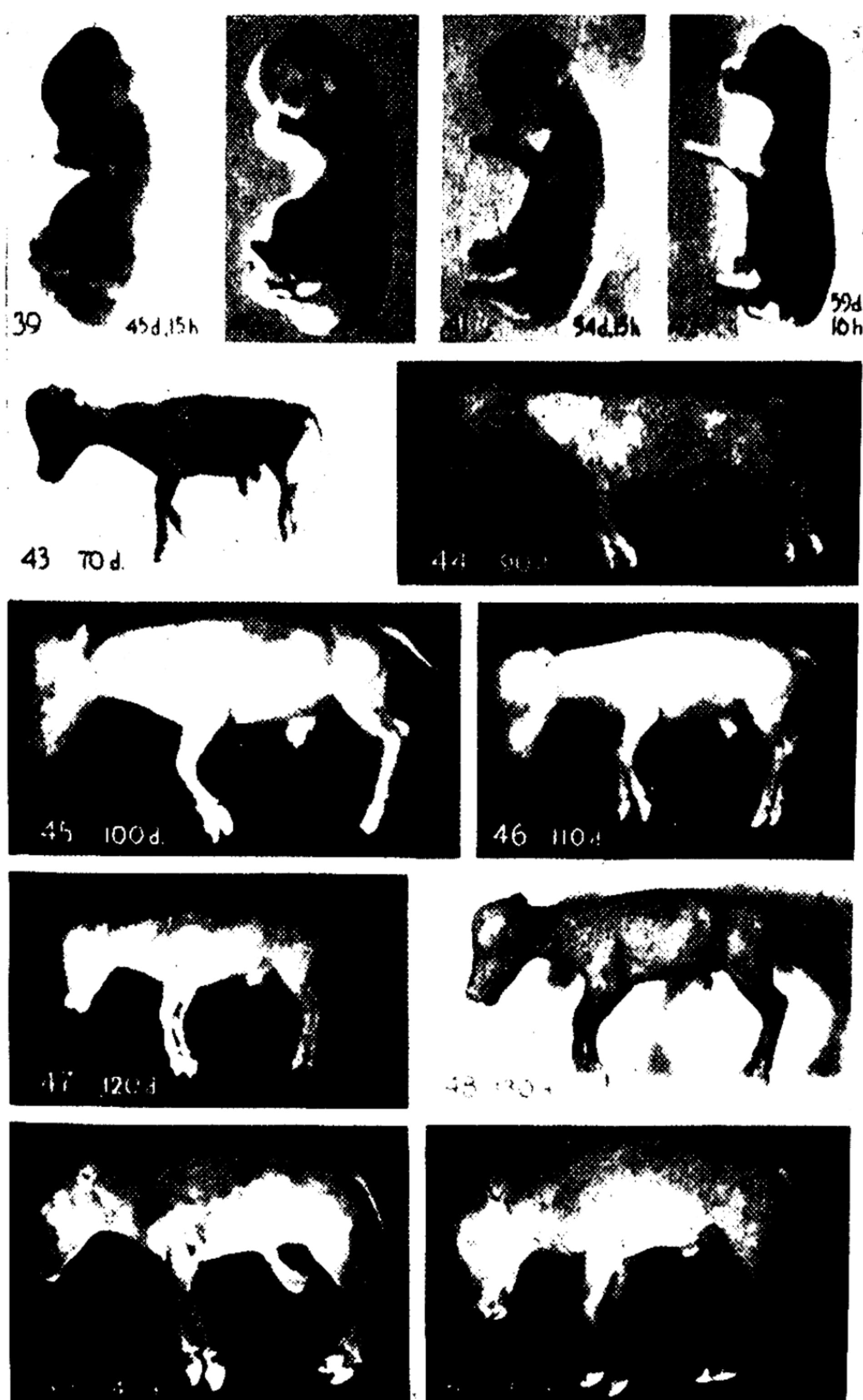


Figure 10.7a. For explanation see Figure 10.7b opposite

multiple births or other causes, is as a rule physiologically and anatomically younger than normal. In particular it is often lacking in the normal development of the heat regulation system (Brody, 1945) and consequently has less power of survival after birth. In the sheep greater losses at lambing are usually met with in twins than in singles, and in lambs from poorly fed than from well fed ewes (THOMSON and FRASER, 1939).

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The prenatal life of an animal may conveniently be divided into three phases, the ovum, the embryonic and the foetal phase (Winters, 1948). The ovum phase lasts from the fertilization of the ovum until implantation or attachment has taken place. During this period,

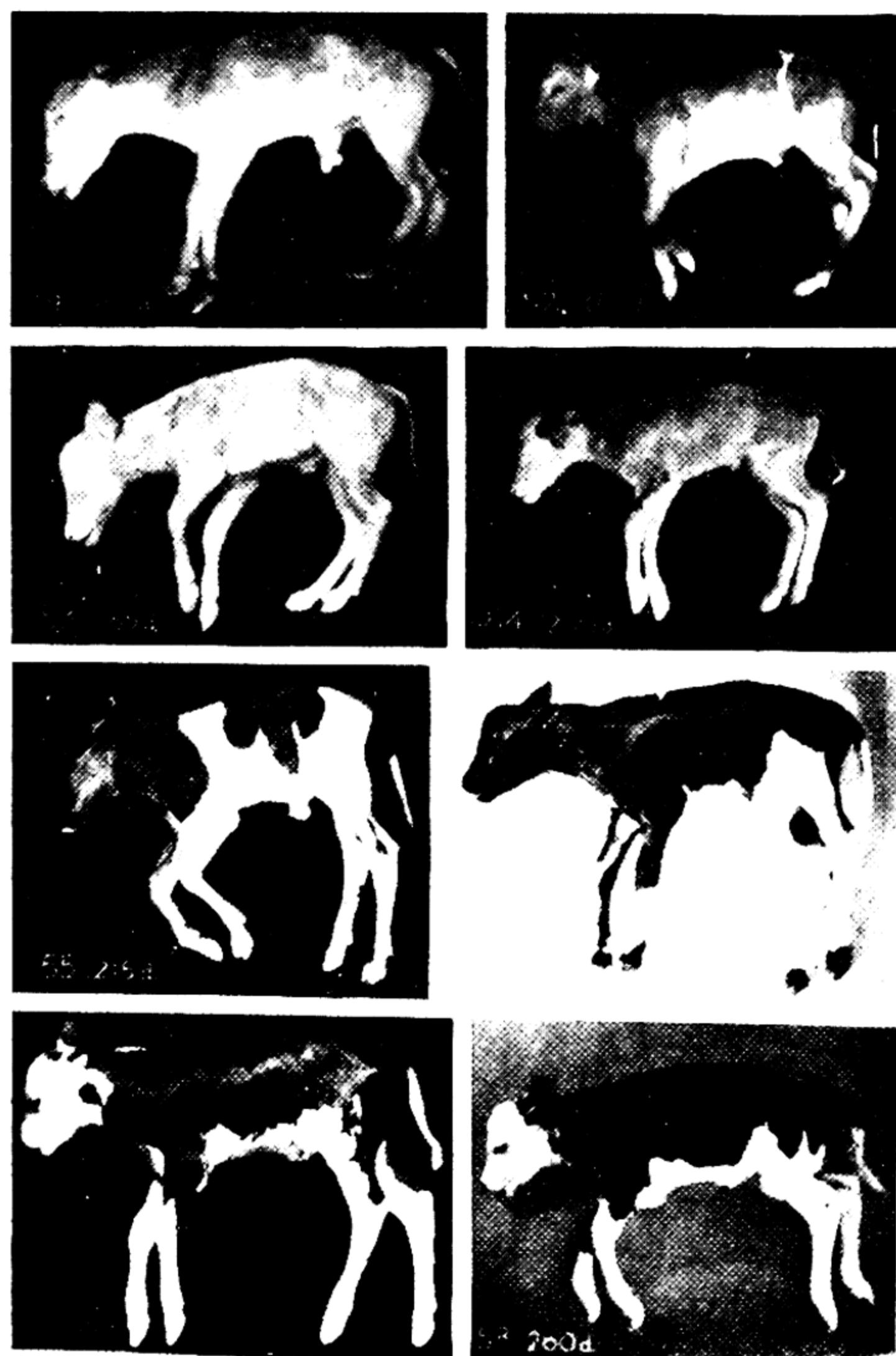


Figure 10.7b. Foetal development in cattle from 39th to 260th day. The age in days is shown on each specimen. Compare with *Figure 10.6* and note the similar pattern of changes in form with age in the bovine and ovine foetus. Relative magnification of specimens: No. 39 $\times 1.1$; No. 40 $\times 0.9$; No. 41 $\times 0.75$; No. 42 $\times 0.5$; Nos. 43 and 44 $\times 0.25$; Nos. 47 and 48 $\times 0.13$; Nos. 55, 56, 57 $\times 0.06$; No. 58 $\times 0.05$. (From Winters *et al.*, 1942, by courtesy of *Univ. Minn. Agric. Exp. Sta. Tech. Bull.*)

which lasts for about 10 days in sheep and 11 days in cattle (WINTERS and FEUFFEL, 1936; WINTERS *et al.*, 1942), little change in shape of the embryo takes place, it retaining an approximately spherical form. The embryonic phase is considered as the time during which the major tissues, organs and their major systems are differentiated; this lasts from about the 10th to the 34th day after fertilization in the sheep

and from the 11th to the 45th day in cattle. During this period the body of the individual undergoes a series of successive changes, though gaining but little in absolute weight. The third phase, the foetal stage, which lasts from the embryonic stage to birth, is characterized by vastly different growth rates or heterogonic growth of the various organs and parts of the foetus, resulting in great and continuous changes in the conformation of the individual (*see Figures 10.6 and 10.7*).

Sheep

In the sheep more knowledge is available on foetal development than in any other farm animal, thanks to the work of Wallace (1948). He studied foetal growth and development in the sheep from conception to the 140th day of pregnancy, or just before birth, by dissecting numbers of foetuses at intervals of 28 days, weighing individual organs, parts and tissues of each foetus. The experimental animals were mature Border Leicester \times Cheviot ewes mated to the same Suffolk ram. The ewes were fed quantitatively and qualitatively adequate rations to cover their requirements for maintenance and reproduction but were not allowed to become over-fat. The results can therefore be considered as typical for normal development of this cross during prenatal life. Wallace found that the foetus as a whole made very little gain in absolute weight until after the 84th day. The average foetal weight was at 28 days 0.53 g., at 56 days 45 g., at 84 days 501 g., at 112 days 1,952 g., and at 140 days 5,866 g. Comparable weight changes of foetuses have also been observed by Winters and Feuffel (1936) in Shropshire \times Hampshire and by a few other workers (for literature, *see* Wallace, 1948).

The carcass of the foetus (head and feet included) gains weight at a similar rate to the organs as a whole from 56 to 112 days, but from 112 to 140 days the organs gain weight at a higher rate and are better developed at birth than the carcass. The individual organs exhibit marked heterogonic growth throughout foetal life which appears to be largely caused by functional necessity. Organs such as the liver, kidneys and the heart, which are presumably of functional importance in foetal life, make a high proportion of their foetal growth in the earlier stages, while others like the alimentary tract, which are not vitally important until birth, make a far higher proportion of their growth in the later stages. The abomasum is by far the most highly developed of the four stomachs at birth; this is clearly functional, for the mother's milk, the sole food of the lamb just after birth, is primarily digested in this part of the stomach. At 56 days the abomasum makes up to 17.2% of the total weight of the four stomachs, while at birth the corresponding figure is 55.8%. The various body regions grow also at widely different rates in foetal life. At 56 days

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the head, for example, accounts for 32.7%, the shoulders 16.6%, and the legs 10.6% of the total carcass weight, while at birth the corresponding figures are for the head 11.3%, shoulders 23% and the legs 22.3%; this indicates a very high relative growth rate in the head during the early stages of foetal life. It also indicates an earlier onset of high growth rate in the shoulders as compared with the legs, though the latter make up for it in the later stages. The different body tissues show also marked heterogonic growth. Nervous tissue is by far the earliest maturing. At 56 days it accounts for 7.5% of the total carcass weight, while at 140 days it makes up only 2.4%. In early foetal life bone has a high rate of growth due to the rapid growth of the skull. Between 56 and 84 days the flesh has a relatively higher growth rate than bone while later and especially after 112 days bone grows again at a relatively higher rate than muscle, chiefly due to the high growth rate of the limb bones at that stage. At 56 days bone accounts for 22.9% and at 140 days 26.6% of the foetal carcass weight. The different skeletal units exhibit marked differential growth in foetal life largely dependent on their relative position in the body. At 56 days the skull is the best developed bone in the body and is 2.1% of its weight at birth, whereas the total skeleton is only 0.67% of its weight at birth. Before the 56th day, the axial skeleton as a whole has a higher growth rate than the appendicular skeleton, due to the early onset of high growth intensity of the skull. Between 56 and 140 days the appendicular skeleton has a higher growth rate than the axial skeleton, the latter declining in growth rate between 84 and 140 days, while the former grows at an increasing rate between 56 and 140 days. Within the axial skeleton there is an early onset of high growth rate at the anterior end passing gradually backwards to the lumbar and sacral vertebrae which do not attain high rate of growth until after birth. Within the appendicular skeleton little differential growth of individual bones is met with before 56 days of foetal life. At that age the proximal bones have made slightly greater relative gain than the distal ones. After this stage marked heterogonic growth of individual bones in a definite distal-proximal order is exhibited. Between 56 and 84 days the cannons have the highest specific growth rate of all the limb bones, from 84 to 112 days the tibia-fibula and radius-ulna have the highest specific growth rate and from 112 to 140 days the femur and the humerus exhibit the highest specific growth rate while the pelvis and the scapula do not attain a high rate of growth until after birth. In early foetal life the bones of the fore-limbs grow at a faster rate than do those of the hind limbs, while at later stages the process is reversed so that at birth the hind limbs are somewhat better developed than the fore-limbs. This is shown in *Figure 10.6* (from Winters and Feuffel, 1936) where the fore-limbs of the foetus are distinctly longer from the

42nd to the 74th day of foetal life, while the hind limbs make up this difference at later stages and attain even greater length than the fore-limbs at birth. Similar changes in form of the lamb during intra-uterine life have also been demonstrated and described by CURZON and MALAN (1935).

The result of the differential growth of the various organs and parts of the foetus in prenatal life is that at birth the lamb is born with large head and long well-developed legs, while the trunk is relatively poorly developed, being short, shallow and narrow, the neck being the best developed part of the trunk.

The hair and wool does not develop to any great extent until in the last few weeks before birth (*see* Chapter 11). The development of the foetus is greatly affected by the plane of nutrition of the mother during pregnancy (*see* page 475).

Cattle

Less is known about the prenatal development of body proportions, as measured by weight, in cattle than in sheep. As, however, these two species are closely related it may safely be assumed that foetal development in both runs broadly along similar lines. Available evidence supports this view. Winters *et al* (1942) have illustrated photographically the changes in body shape occurring during the foetal phase in cattle, *i.e.* from the 45th day after conception to birth (*see Figure 10.7*). These changes are, as judged by eye, very similar to those in the sheep (*see Figure 10.6*). Due to the longer gestation in the cow, however, it takes the foetus a longer time chronologically to undergo comparable morphological changes. In the early foetal stage the head is relatively very large while the limbs are as yet very small. At the 54th day the limbs have already increased considerably in length and the fore-limbs more so than the hind limbs. At the 59th day there is apparently a greater difference between the length of the limbs in favour of the fore-limbs than at any other stage. This difference then gradually disappears due to a higher growth rate in the hind limbs in the later stages of foetal life and at birth the hind limbs are slightly longer than the fore-limbs. This is essentially the same pattern of development as in the sheep (page 445 and *Figure 10.6*). In the middle stages of foetal life (from 100 to 200 days) the facial parts of the head develop rapidly, while in the last stages the upper parts of the limbs and the trunk develop rapidly relative to the head. The hair coat does not cover the body until at 230 days. Winters *et al* (1942) have shown that in the general appearance of body form, the 140-day bovine foetus is comparable with 104-day sheep foetus, indicating that the former undergoes the early developmental changes in relatively shorter time than the ovine foetus. As in the sheep the bovine foetus makes very little actual gain in weight during the first

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half of uterine life; at 55 days it weighs less than 10 g. and at 135 days some 1,400 g., the greatest gain being made during the last third of

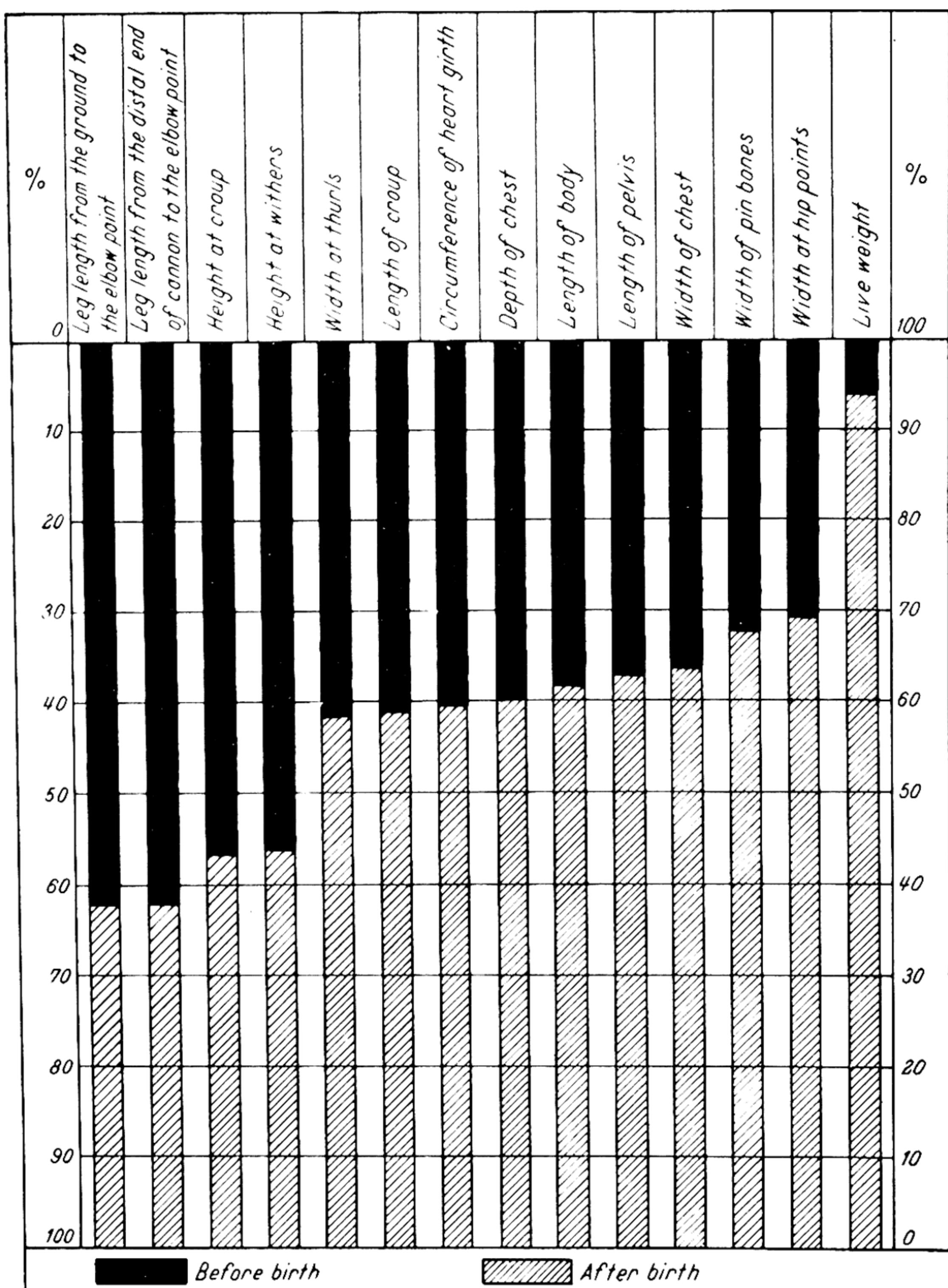


Figure 10.8. Prenatal and postnatal development of body measurements and weight in Norwegian cattle. Liveweight and measurements at birth expressed as percentages of the same at maturity (5 years), showing proportionately much better development of all body measurements than weight at birth and of the former the leg length is best and the width of hips poorest developed at birth. (From Isaachsen, 1933, by courtesy of *Meld. fra Norges Landbrukshøjskole*.)

prenatal life (BERGMANN, 1921; HAMMOND, 1927; KISLOVSKY and LARCHIN, 1931; WINTERS *et al.*, 1942).

At birth the various body parts have attained vastly different

proportions of their size at maturity. Isaachsen (1933) has shown the weight and several body measurements at birth as a percentage of the same measurements at maturity (5 years) in cattle (*Figure 10.8*). The calf at birth weighs but 6.5% of the mature weight, while at that age the leg length is 63%, the height at croup 57%, the height at withers 56%, the width of chest 37% and the width at hips 31% of the same measurements at maturity, the leg length being the best and the width at hips the least developed at birth. The difference in the relative development of the leg length and the height at withers indicates the earlier development of the distal part of the limb as compared with the proximal part and the trunk. The difference in relative development of the height at croup and the height at withers shows the slightly better development of the hind limb as compared with the fore-limb at birth (page 446, *Figure 10.7*). Brody and Ragsdale (1924) observed similar development of calves at birth though in their case the differences between the various measurements, especially in the later maturing ones at birth and at maturity, were still greater, probably due to the more advanced ultimate development of American breeds of cattle. BROVAR (1944) has found that the skeleton of the calf attains its maximum proportions of the body weight at birth.

Horses

The actual amount of growth made by the foal in the early foetal stage is small, but from the middle of pregnancy onwards it increases at an ever-increasing rate (Hammond, 1952a). As a result of the long pregnancy period in the mare—approximately 11 months—the foal at birth has reached a higher degree of development than the newborn of any other species of farm animal, as previously stated (page 438); it is able to run about a few hours after birth. At birth the legs of the foal are so well developed that little growth in length occurs below the hocks after birth. The adult size of a horse can as a rule be estimated by the length of the cannons and pasterns at birth. Proper feeding of the mare during the latter half of pregnancy is of great practical importance, as under-nutrition at that stage will result in a shortening of the legs of the foal at birth; this may result in a permanent stunting in size due to the natural high growth intensity in the distal bones of the limbs in prenatal life and to their rapidly decreasing growth rate in postnatal life (*see* page 517).

Isaachsen (1933) has demonstrated the proportional development of the foal at birth by showing the weight and various body measurements as a percentage of those at maturity (*Figure 10.9*). At birth the foal has attained 9% of the weight of the adult horse, 73% of the leg length (from ground to the elbow joint) and 60% of the height at withers. These figures indicate the greater relative development of

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the foal as compared with the calf at birth (page 448 and *Figure 10.8*). The greater proportional difference at birth in the leg length (73%) than in the height at withers (60%) as compared with the depth of the chest (46%) shows the relatively greater development of the legs in foetal life (see also page 517).

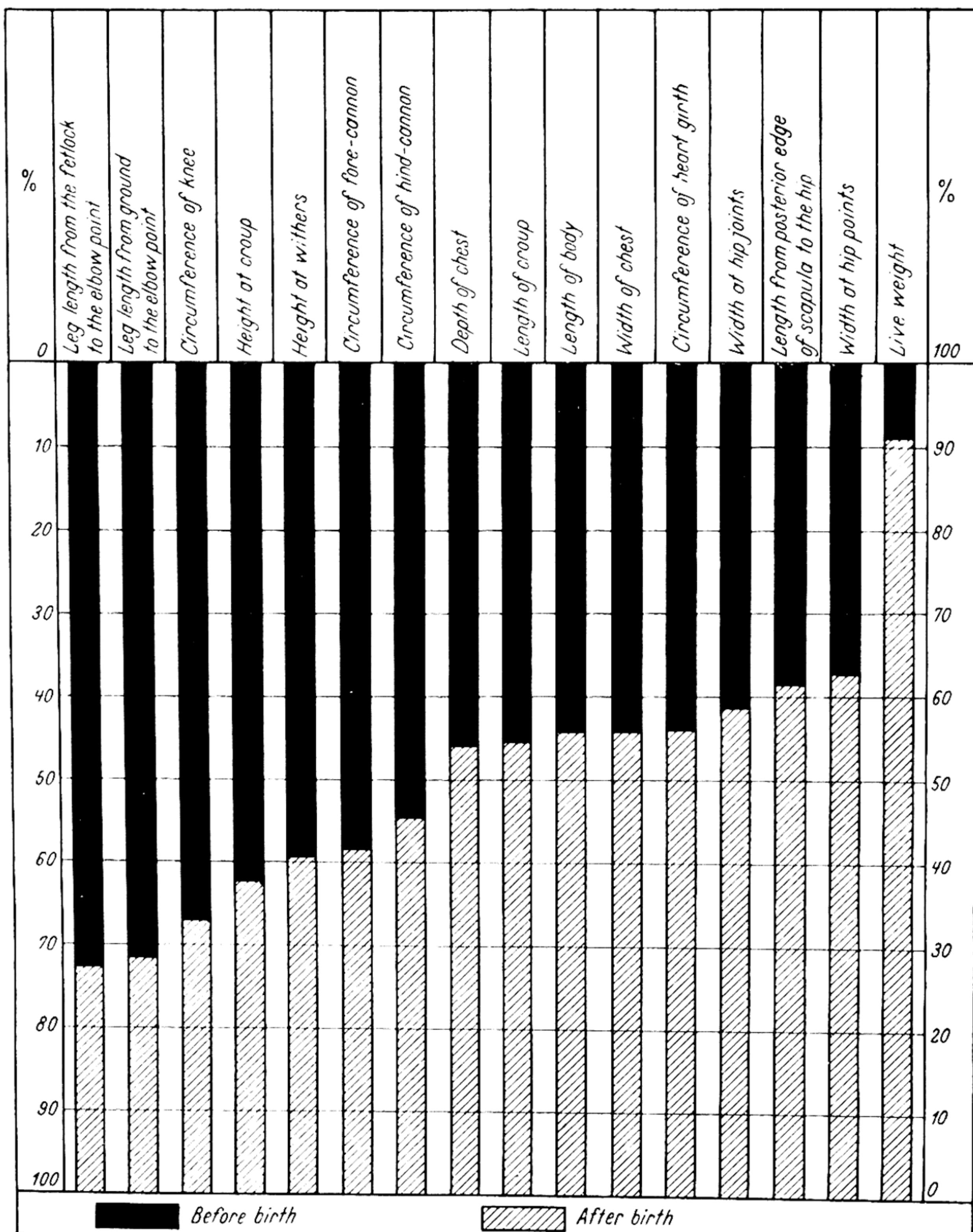


Figure 10.9. Prenatal and postnatal development of body measurements and weight in the horse. Liveweight and measurements at birth are expressed as percentage of the same at maturity (5 years). Compare with *Figure 10.8* and note the more advanced development of the foal than the calf at birth, particularly the proportionately greater leg length relative to height at withers in the foal. (From Isaachsen, 1933, by courtesy of *Meld. fra Norges Landbrukskjole*.)

Pigs

No single factor is as important in determining the birth weight and general development of pigs in foetal life as the number of piglets per litter. The larger the number per litter the smaller the average weight per piglet and greater the variations in weight within litters. The smaller piglets at birth are invariably less well developed than the larger ones and more likely to die (for references, *see* page 439).

Lowrey (1911) studied developmental changes in the pig during intra-uterine life and not knowing the exact age of the foetuses he used their length as a criterion by which to compare the relative development of the various organs. He found the same general trend of development as Wallace (1948) later found in the sheep. At the earliest stage examined (foetuses of 15 mm. length) the foetal organs, including brain and spinal cord, had their maximum relative size, accounting for 38% of the total body weight. At the same stage the heart attains its maximum relative size, 4.6% of the total body weight, and this declines to about 1% at birth. Just a little later (at 18 mm. body length) the head and the brain have attained their maximum relative size, the former making up 30% and the latter 9% of the total body weight, corresponding figures at birth being 22% and 4%. Somewhat later, though early in the foetal stage, the liver followed by the kidneys, the eye-balls, and the lungs attain their maximum relative size, while the spleen, pancreas and thymus glands do not reach their maximum relative size until shortly before birth (at 215 mm. body length). The stomach and intestines (empty) increase proportionately relative to other organs and the body as a whole throughout the prenatal period attaining 3.6% of the body weight at birth. That the pig is born anatomically younger than the lamb is evident from the fact that the head makes up a much higher proportion of the body weight at birth in the pig than in the lamb and the limbs in the pig, though relatively better developed at birth than the trunk, have not attained the same degree of development as in the sheep (Wallace, 1948; McMeekan, 1940, 1941).

Poultry

During the prehatching period the chick undergoes rapid developmental changes. As in mammals, the head and especially the brain and the eyes are very early maturing as well as some of the vital internal organs. LATIMER (1932) found that at hatching the central nervous system and the head make up greater percentages of the body weight than at any later age and the skeleton and the viscera as a whole account for a higher percentage of the body weight at hatching than in the adult, indicating the early maturity of these parts as compared with the muscular and fatty tissues. At hatching the legs are better developed than the wings and than the depth of the body. In the

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appendicular skeleton, as in mammals, a growth gradient is observed with an early onset of high growth rate in the distal bones passing up the limbs (WILSON, 1952).

POSTNATAL CHANGES IN DIFFERENT SPECIES

As an animal grows up from birth to maturity great changes occur in its body proportions or conformation (*Figure 10.4*). Hammond (1932a) and Pálsson and Vergés (1952) in the sheep, and McMeekan (1940, 1941) in the pig, have found these changes to be a result of differential growth gradients between the different parts and tissues of the body, taking place in a definite order throughout the growing period. The normal developmental changes with age can only be demonstrated accurately by feeding the animal on an optimal level of nutrition throughout the growing period, thus enabling it fully to exhibit its inherent growth capacity. This is because a low plane of nutrition during a certain time interval or during the entire growing period not only retards growth and prolongs the growing period, but also distorts the animal's form to a varying extent depending on at what stage of development and to what degree it was subjected to under-nutrition. It may even result in permanently changing its body proportions (for literature, *see* McMeekan, 1940, 1941; Pálsson and Vergés, 1952).

Sheep

Pálsson and Vergés (1952) studied developmental changes in the sheep from birth to mature weights, by killing and dissecting a number of Suffolk \times Border Leicester-Cheviot lambs of balanced sexes at three ages, birth, 9 weeks and 41 weeks. These lambs were reared on a high plane of nutrition from the 90th day of intra-uterine life until killed so that the last group killed at 41 weeks had almost ceased growing and had reached mature weights of 215.5 lb. and 144.7 lb. for wethers and ewes respectively. Their results in brief were as follows: with an increase in age and weight the dressed carcass makes up an increasing proportion of the live weight, the dressing out percentage increasing from 45% at birth to 48.9% at 9 weeks and 59.7% at 41 weeks. This is due to the higher growth rate of the carcass tissues, especially muscle and fat, than that of the organs and offal parts as a whole. The relative development of the carcass shown as a percentage of live weight is, however, partly masked by the great increase in the contents of the alimentary tract after birth. As a percentage of empty (minus contents of alimentary tract) live weight, the carcass increases from 48.7 at birth to 57.0 at 9 weeks and 64.4 at 41 weeks. As most of the increase in relative carcass weight consists of edible meat these changes are of great importance to the meat producer. The head as a percentage of live weight decreases from

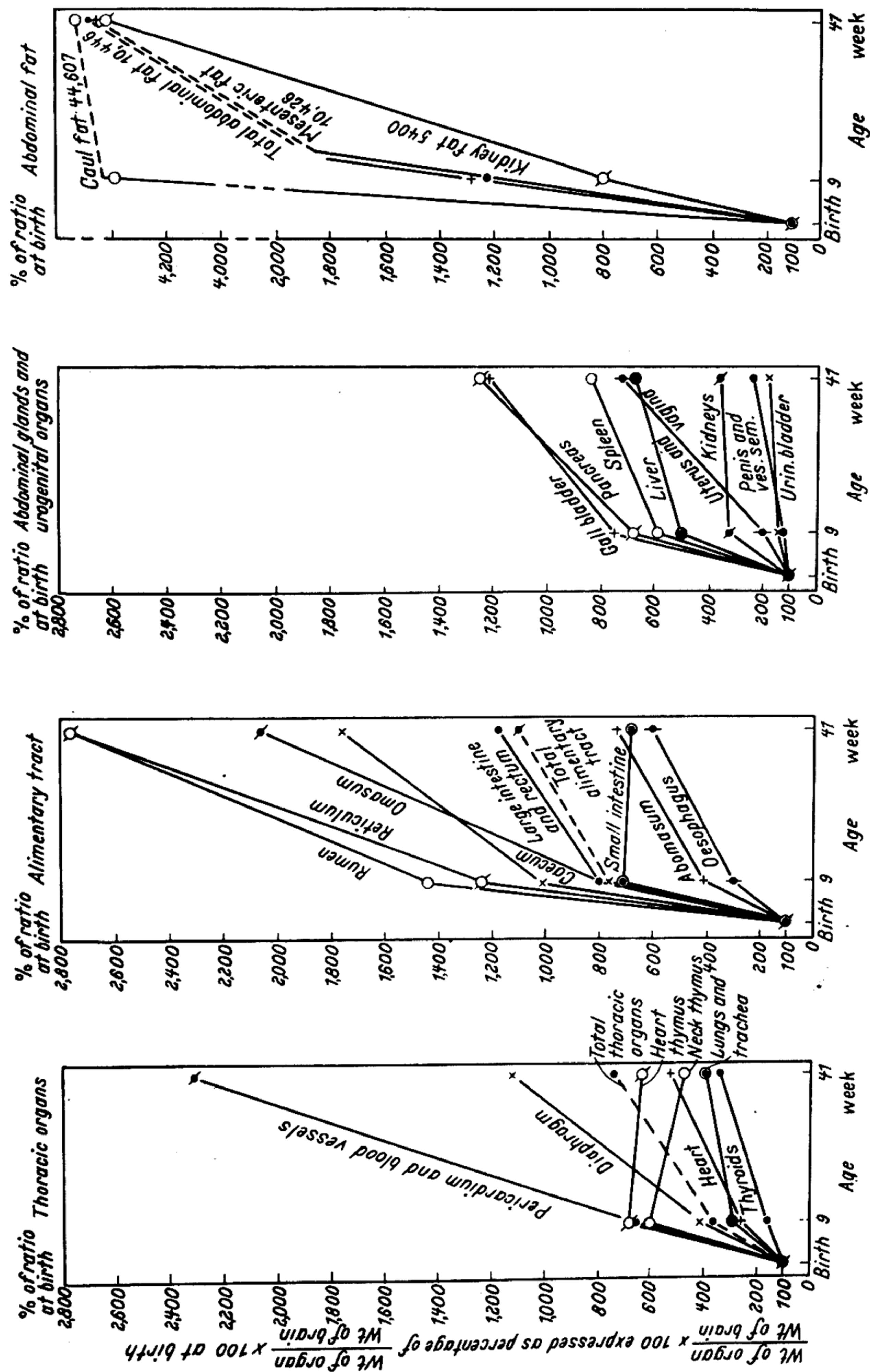


Figure 10.10. Postnatal growth of organs in lambs on a high plane of nutrition relative to brain weight, showing great variation in their relative rate of growth. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

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8.1% at birth to 2.5% at 41 weeks, indicating its very much slower rate of growth than that of the carcass in postnatal life.

The brain and the eyes make relatively smaller gain in weight than any other parts or tissues of the body in postnatal life. The brain, however, is still earlier maturing than the eyes; it does not quite double its weight from birth to 41 weeks, while the eyes weigh three times more at 41 weeks than at birth (Table 10.1).

TABLE 10.1
AGE CHANGES IN THE MEAN WEIGHT (G.) OF THE BRAIN AND THE EYES (Pálsson and Vergés, 1952)

	Birth	9 weeks	41 weeks
Number of individuals	2	8	4
Brain	58.3	88.4	105.6
Eyes	9.0	17.9	27.0

Due to the early maturity of these organs, Pálsson and Vergés used either or both of them as standards for comparison of the development of other organs, parts and tissues of the body. The weight of each organ or part was expressed as a percentage of the standard organ at the same age.

The various internal organs exhibit marked differential growth in postnatal life. Their order of development relative to the brain is shown in *Figure 10.10*. As stated above (page 437), the heterogonic growth of the individual organs appears to be primarily functional. Those organs of most vital function to the life of the animal like the brain, eyes, lungs, kidneys, heart, oesophagus, abomasum and small intestines are relatively well developed at birth and consequently grow proportionately less in postnatal life than organs like the rumen and reticulum, which have an unimportant function until some time after birth, when the lamb begins to eat fibrous foods, or those whose function is largely that of storage of nutrients such as the abdominal fat depots, which develop mainly in the later stages of growth.

In postnatal life the different joints or body regions develop in a definite order of increasing growth rate from the head and feet to the loin region (*Figure 10.11*). The feet followed by the head grow at a much slower rate than any of the carcass joints, increasing their birth weight only 2.6 to 3.7 times respectively relative to the brain-plus-eyes from birth to 41 weeks, whereas the legs and the loin, the carcass joints of the lowest and the highest growth rate, increase their birth weight 11 and 25.9 times respectively, relative to the brain-plus-eyes during the same period.

The major body tissues exhibit also marked differential growth rates in postnatal life (*Figure 10.12*). The order of increasing growth

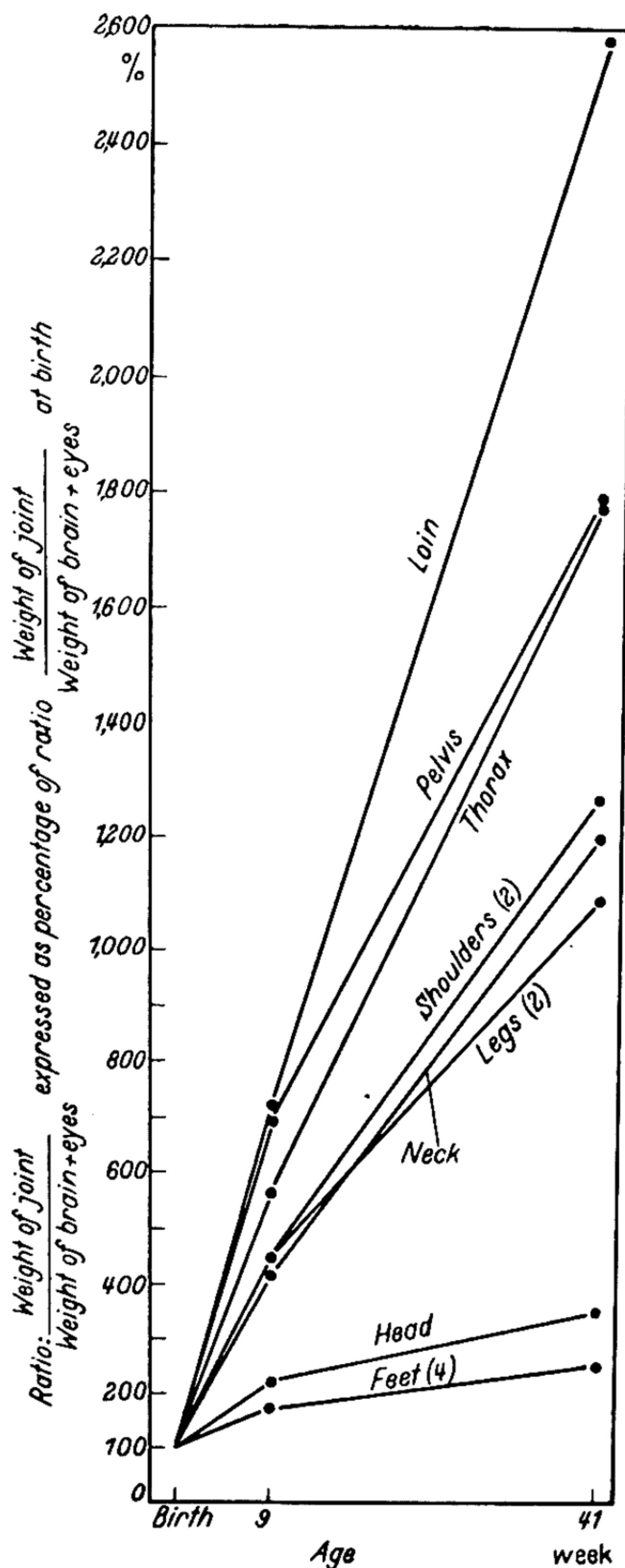


Figure 10.11. Postnatal development of different joints in lambs relative to brain + eyes, showing a gradient of increasing growth rate from the head and feet to the loin region. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

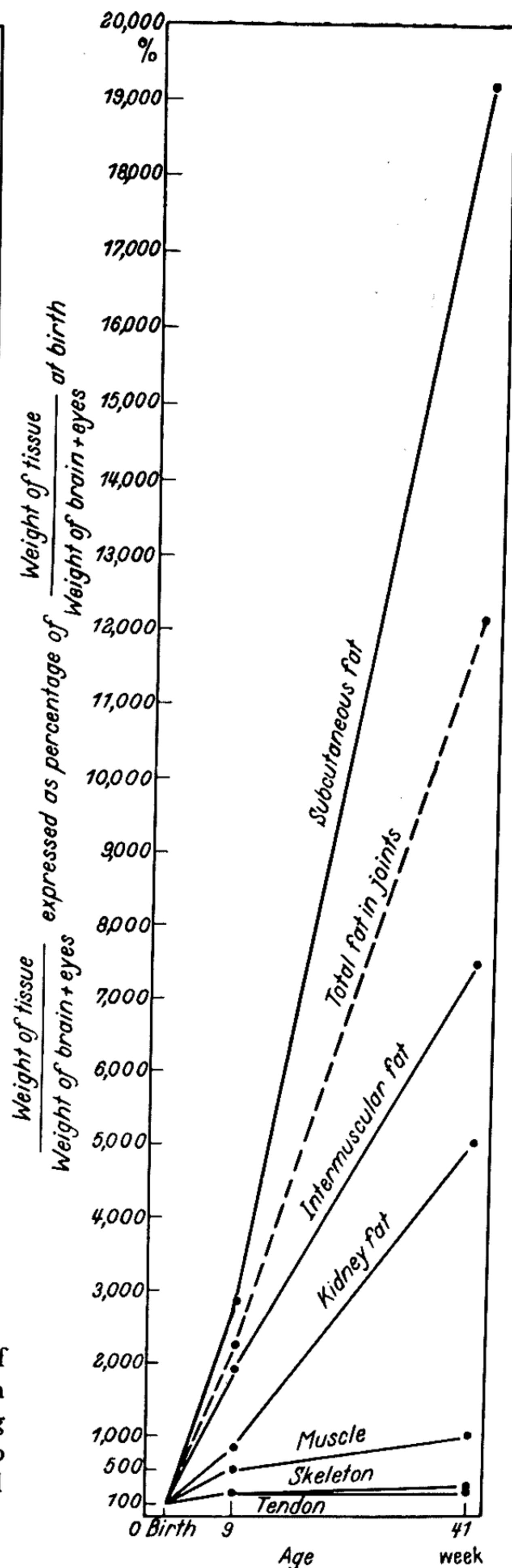


Figure 10.12. Postnatal development of the major tissues of lamb carcasses relative to brain + eyes, showing an outward order of increasing growth rate from the nervous tissue to bone, muscle and fat. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

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rate with age follows an outward trend from the central nervous system to bone, tendon, muscle, intermuscular fat, and subcutaneous fat. Consequently the early maturing nervous tissue and the skeleton make a greater proportion of their growth earlier in life than do muscle and fat; the latter, particularly subcutaneous fat, does not develop to any great extent until late in the growing period.

Within any of the major tissues, bone, muscle and fat, well-defined gradients also exist. Within the skeleton, in postnatal life, waves of increasing growth intensity pass from centres of early (foetal) maximum rate of growth near the extremities towards the central region of the body. The order and magnitude of this differential growth with age in the different skeletal units is illustrated in *Figure 10.13*. In the

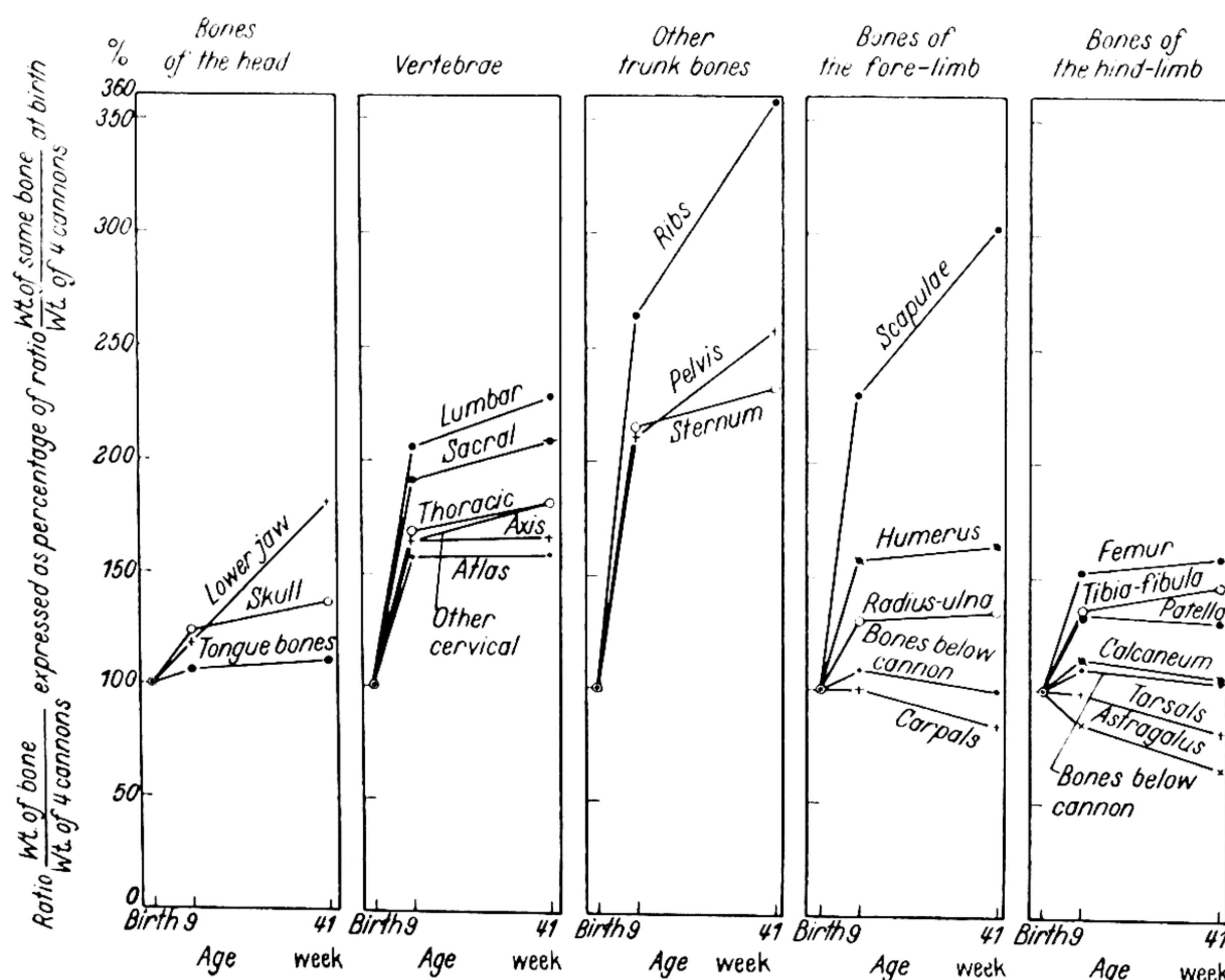


Figure 10.13. Postnatal development of the skeleton in lambs relative to the weight of the four cannon bones, showing early maturity of the appendicular as compared with the axial skeleton and gradients of increasing growth rates from the skull and the carpal and tarsal regions to the central regions of the body—the lumbar vertebrae and the ribs—and to the extremities. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

axial skeleton, the skull, or rather the cranium, is the earliest developing part, and from it waves of increasing growth intensity pass backwards to the lumbar region and downwards to the nose and lower jaw. In each limb, similar growth waves pass with age from the early developing metacarpals and metatarsals down to the distal bones and

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up towards the lumbar region, the pelvis and the scapula being later developing than the femur and the humerus. The ribs are the latest maturing bones of the body. The bones of the fore-limb, as a whole, are somewhat later maturing than those of the hind limb. Both growth in length and thickness of the long bones of the limbs follow the same trend as growth in weight. The upper bones increase relatively more both in length and thickness than the cannons in postnatal life, and growth rate in length attains its maximum at an earlier age than growth rate in thickness.

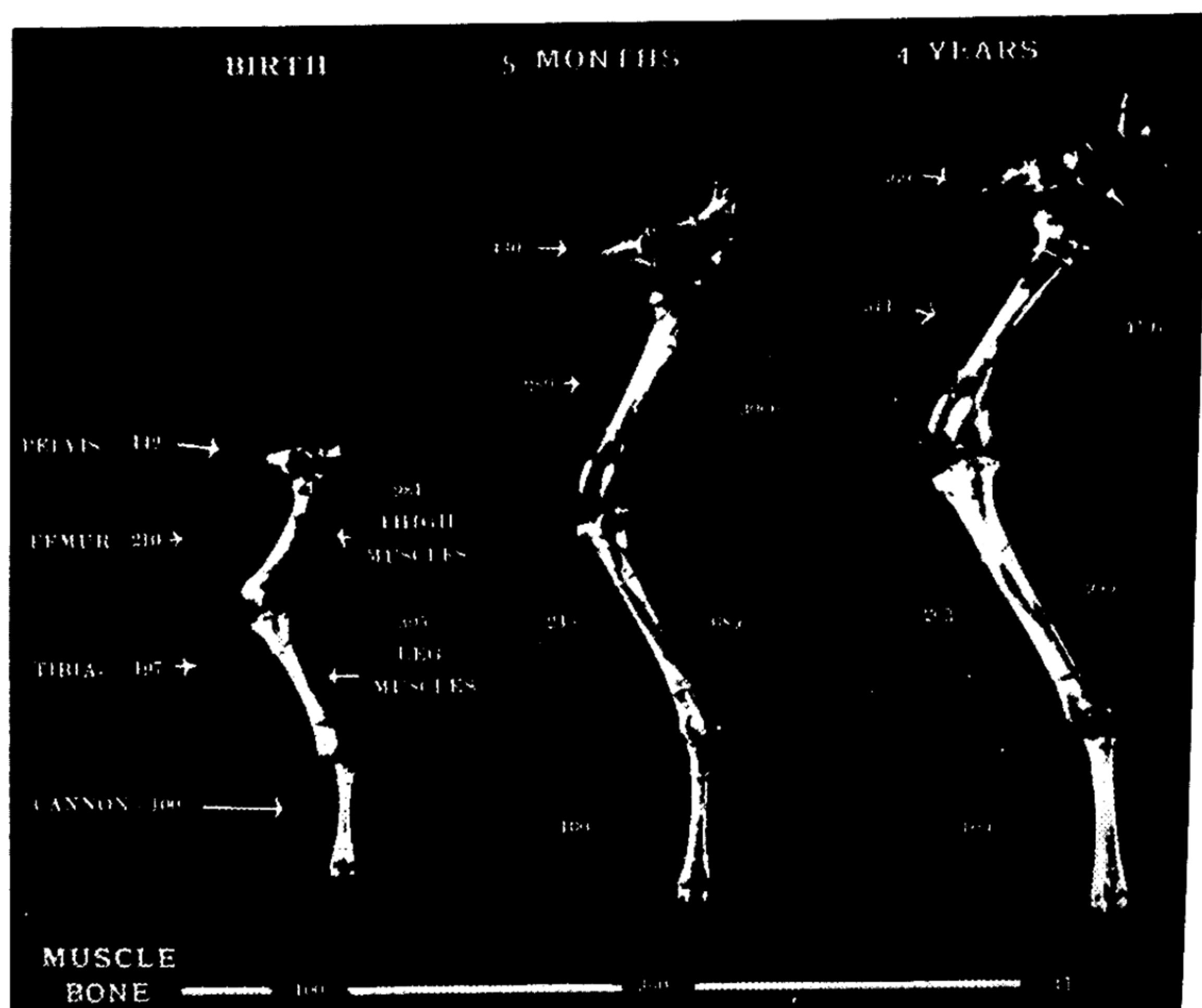


Figure 10.14. Age changes in the proportions of the parts in the leg of Suffolk ewes. The weights of the bone and the muscles are shown as a percentage of the weight of the cannon bone in each case. (From Hammond, 1932a, by courtesy of Oliver and Boyd.)

The development of muscle and fat in the different body regions is also governed by growth gradients similar to those met with in the skeleton. For each of these tissues a wave of increasing growth intensity passes with age from the head and neck backwards and from the lower parts of the limbs (arms and legs) upwards to the loin region. Hammond (1932a) has demonstrated the upward gradient of increasing growth rate with age within each tissue as well as between tissues in the leg of Suffolk ewes (*Figure 10.14*). At birth the femur is only 210% of the cannon bone weight while in the adult it is 311%.

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At birth the muscle is only 162% and fat 8% of the bone weight, while corresponding figures in the adult are for muscle 645% and for fat 165%.

As a result of the differential growth of the constituent parts and tissues of the body described above, the full grown sheep has attained, in contrast to the newborn lamb, a rather long, deep and thick-set body with well developed rump and loin (*Figure 10.4*).

In an early maturing animal, the developmental changes take place in much shorter chronological time and are extended further than in a late maturing one. Under similar environmental conditions larger breeds are as a rule later maturing than breeds of smaller size

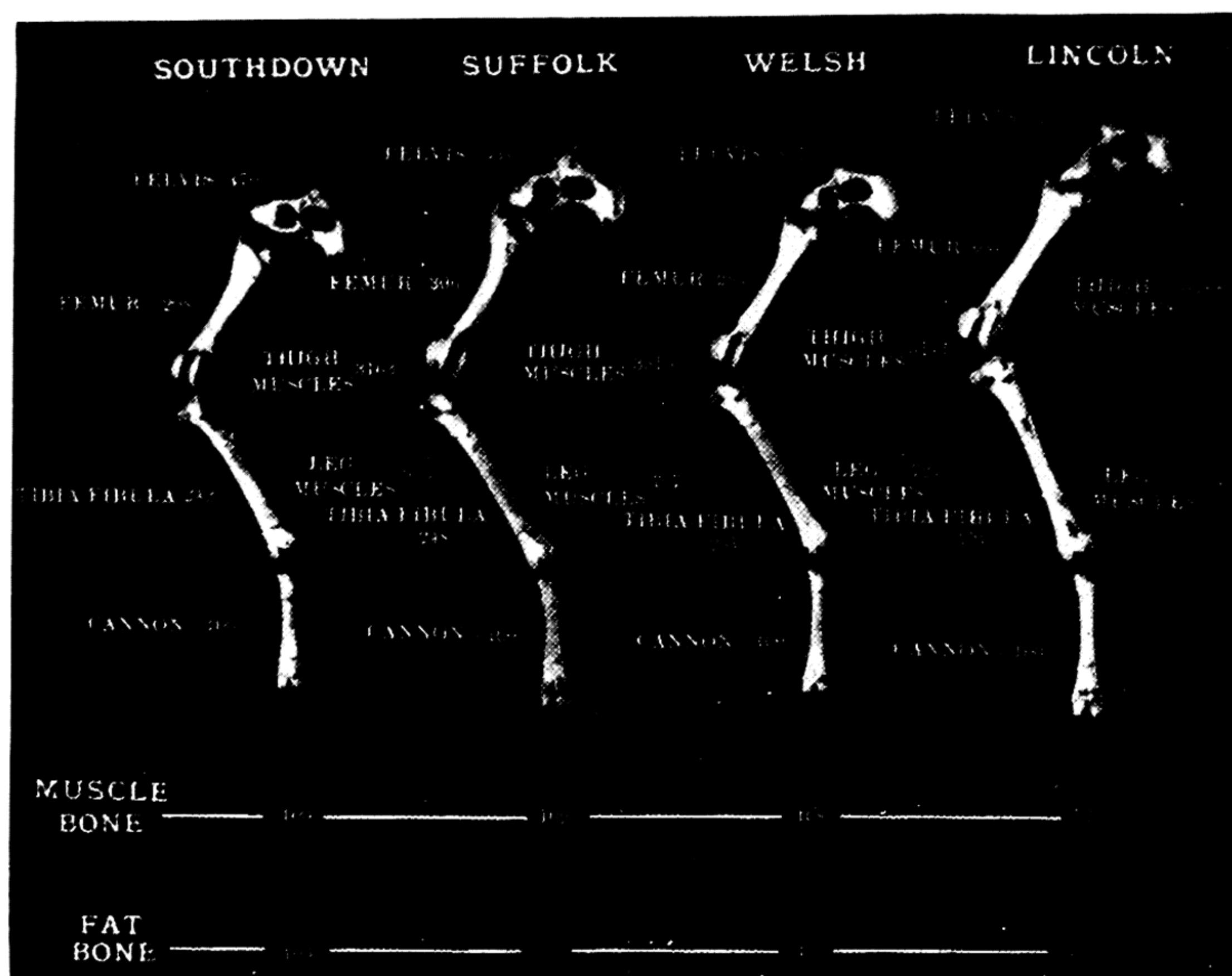


Figure 10.15. Effects of early and late maturity of the breed on the proportions of the parts of the leg in wethers at five months old. The weights of bones and muscles are shown as a percentage of the weight of the cannon bone in each case. (From Hammond, 1932a, by courtesy of Oliver and Boyd.)

(Hammond, 1932a). In sheep, even between improved breeds, there are considerable breed differences in the rate at which changes in the body proportions occur (*Figure 10.15*). At 5 months, in a leg of a Southdown (small early maturing) wether, muscle is 503% and fat 201% of the bone weight, whereas in a leg of a Lincoln wether (large, late maturing) of the same age the corresponding figures are 366% for muscle and only 99% for fat.

Cattle

In cattle (*Figure 10.16*), changes in conformation from birth to maturity are of similar nature to those described above for sheep. Breed differences, however, exist in the rate and extent to which these changes occur. The beef breeds go through these developmental changes more quickly and further than do dairy breeds, with the result that the former have higher dressing out percentage, are lower on the leg, with shorter head and neck and have better developed body, especially the late maturing parts and tissues (loin and rump, muscle and fat) than the latter (KENNEDY *et al*, 1905; HAMMOND, 1920) (*see* page 517).

Postnatal changes in external body measurements in cattle indicate early maturity of the head and the limbs as compared with the trunk. Expressed as percentage of the measurements at birth, the measurements of the skull and the leg length, followed by the height at the withers and at the croup increase least in postnatal life. In contrast, the measurements of the width of the hindquarters make the greatest gain, while those of the length and the depth of the body are in an intermediate position (*Figure 10.8*). The skull and height measurements make most of their postnatal gain in the early stages, followed by the length and depth of the body while the width measurements continue to gain at a relatively high rate until the animal approaches maturity (for literature, *see* Brody and Ragsdale, 1924; Hansen, 1925; Reimer, 1927; BARTLET and JAMESON, 1932; Isaachsen, 1933; BONNIER and HANSSON, 1946; BONNIER *et al*, 1948; HANSSON and BONNIER, 1950; and HANSSON *et al*, 1953). From birth to $2\frac{1}{2}$ years, Reimer (1927) found that, taking the gain in the height at withers as 100, the height at croup increased 99%, length of body 126%, depth and width of chest 138%, width of hips 164%, width between pin bones 200% and the distance from ground to knee 80%.

BROVAR and LEONTJEVA (1939) found growth gradients in the skeleton of cattle of similar nature as described above in the sheep, indicating an earlier maturity of the appendicular than of the axial skeleton and an anterior-posterior gradient of increasing growth rate in the latter and a distal-proximal gradient in the former.

Horses

In the horse, changes in body proportions in postnatal life are of the same order as in cattle. Relative to the measurements at birth, the height measurements increase least and the width measurements most, while length of body and depth of chest are in an intermediate position (Isaachsen, 1933; SCHMIDT and LAUPRECHT, 1928). As in cattle, the height measurements make most of their postnatal gain in the first 8 months after birth, while the width measurements as well as the distance from the posterior edge of scapula to the hip continue

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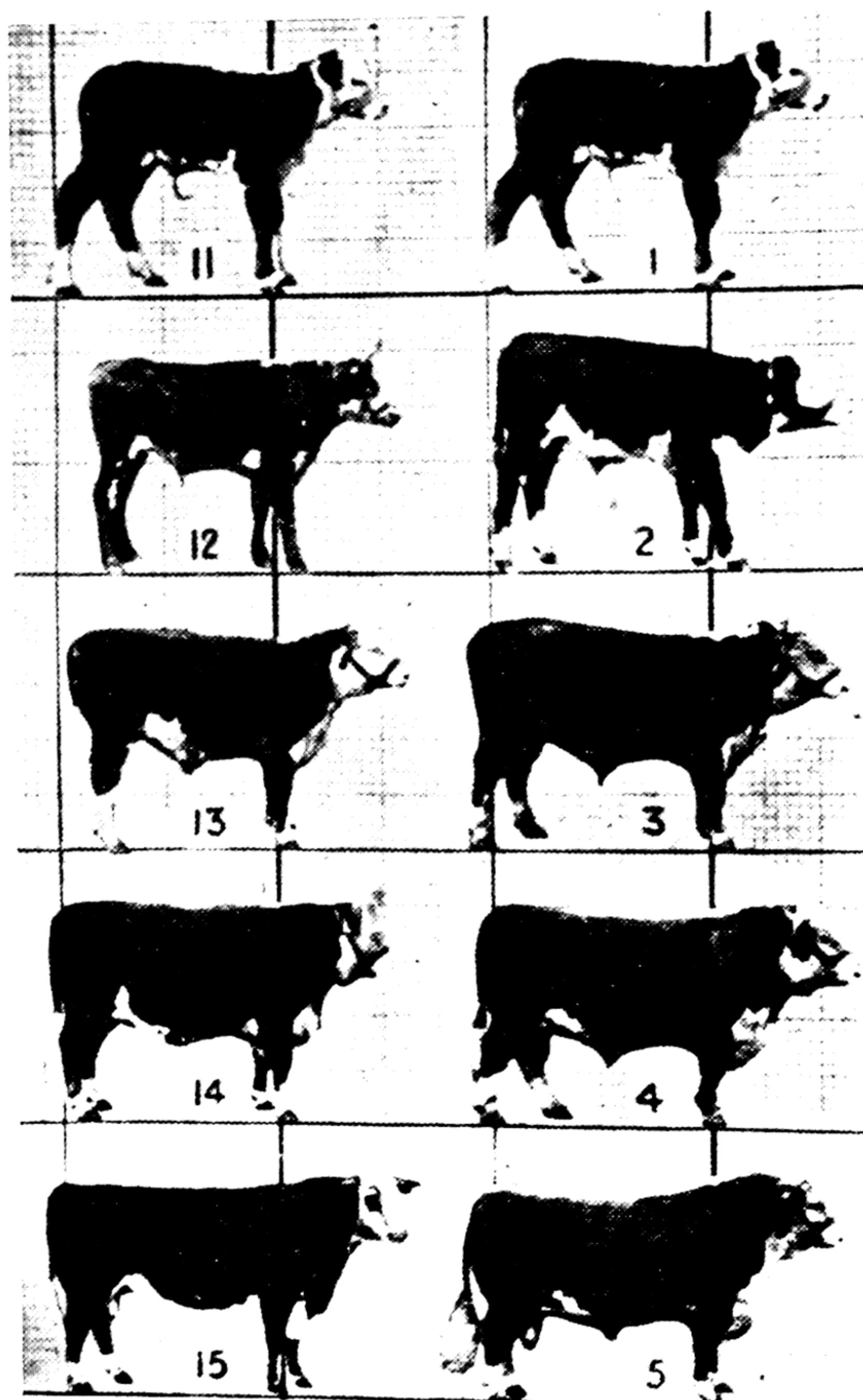


Figure 10.16. Changes in the body proportions of Hereford cattle. All photographs are reduced to the same height at the shoulders in order to show changes in proportions as distinct from size.

(11) Bull, 2 days.	(1) Bull, 2 days.
(12) Steer, 30 months, grown on low level of nutrition.	(2) Bull, 5 weeks.
(13) Steer, 11 months, grown on high level of nutrition.	(3) Bull, 13 months.
(14) Steer, 22 months, grown on high level of nutrition.	(4) Bull, 22 months.
(15) Bull of 100 years ago.	(5) Bull, 5 years.

(From Hammond, 1935, by courtesy of *Emp. J. exp. Agric.*)

to gain at a relatively high rate until the animal reaches maturity, the total length of body and the depth of the chest are in an intermediate position (*Figure 10.9*). Due to the fact that the foal is born in a more advanced state of development than the calf the magnitude of the postnatal changes in body conformation is not so great in the horse as in cattle. In the horse at maturity the leg length is only 1.38 times, the depth of chest 2.13 times, and the width of hips 2.68 times greater than at birth, while in cattle the corresponding figures are 1.60, 2.50 and 3.30 (Isaachsen, 1933).

Pigs

In the pig, as it grows up, changes in body proportions occur, as in other farm animals. At birth the head and feet are relatively large, while the body is very short and shallow and the hind quarters particularly poorly developed, but with increased age and weight the body increases first in length and later in depth and thickness (*Figure 10.17*). McMeekan (1940) found that the changes in conformation with age in the pig are in general a result of similar growth gradients in the different parts, tissues and organs of the body as described above (pages 451-457) in the sheep. However, slight species differences are observed. In the pig, contrary to what is found in the sheep, the hind limbs are later maturing than the fore-limbs, the former making proportionately greater gain in postnatal life than the latter. Changes in body proportions as well as the changes in relative development of the different tissues in postnatal life are more pronounced in the pig than in the sheep, due to the very immature state in which the pig is born (McMeekan, 1940, 1941; HAMMOND, 1922; HOGAN *et al*, 1925).

Early and late maturity in the pig, as in other farm animals, depends on the extent and the rate at which changes in body proportions, and changes in the proportions of the different tissues, occur. In this species the correct fat : muscle ratio is of even greater importance than in other species which are less liable to become overfat. This is made use of in selecting suitable breeds for pork and bacon production (*Figure 10.17*). The pork type is earlier maturing and passes through the growth changes more quickly and to a further extent than the later maturing bacon types (HAMMOND, 1932b; HAMMOND and MURRAY, 1937). At 100 lb. live weight a pork type, like the Middle White, has well developed hams and is well finished, while at that weight a late maturing type, like the Large White, is still growing in length, has poorly developed hind quarters and high proportion of bone (*Figure 10.18*). At 200 lb. live weight, the usual weight for bacon, the Middle White has attained too high a degree of development; the side is too deep relative to its length and too fat to give first quality bacon. At that weight, however, the Large White

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has the ideal form and proportions of lean to fat for bacon, at this stage having much the same body proportions and fat : muscle ratio as the Middle White has at 100 lb. live weight.

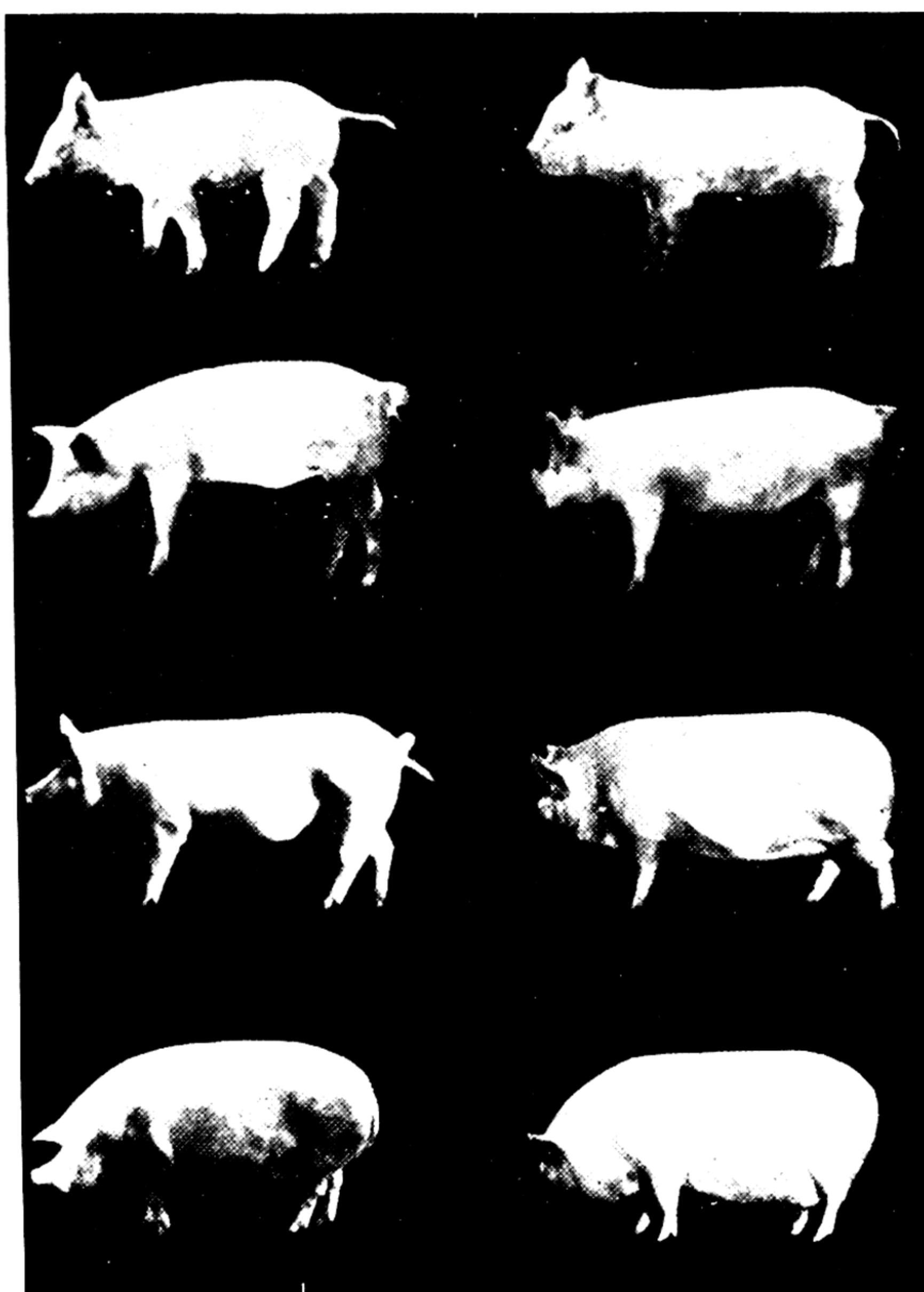


Figure 10.17. Postnatal changes in body proportions of the pig. In order to compare changes in proportions as distinct from changes in size all the animals have been reduced to the same height at the shoulders. The pork breeds such as the Middle White (right) pass through the growth changes more quickly than the bacon types such as the Large White (left). *Top line*—1 week old. *2nd line*—100 lb. (Pork weight). *3rd line*—200 lb. (Bacon weight). *Bottom line*—Adult. (From Hammond, 1932b, by courtesy of *J. Roy. agric. Soc.*)

Poultry

In poultry, changes in body proportions occur from hatching to maturity in much the same way as in domestic mammals (MITCHELL *et al*, 1926, 1931; LATIMER, 1924, 1932; CSUKAS, 1935; WILSON, 1952). Age changes in external body measurements from hatching to 24 weeks

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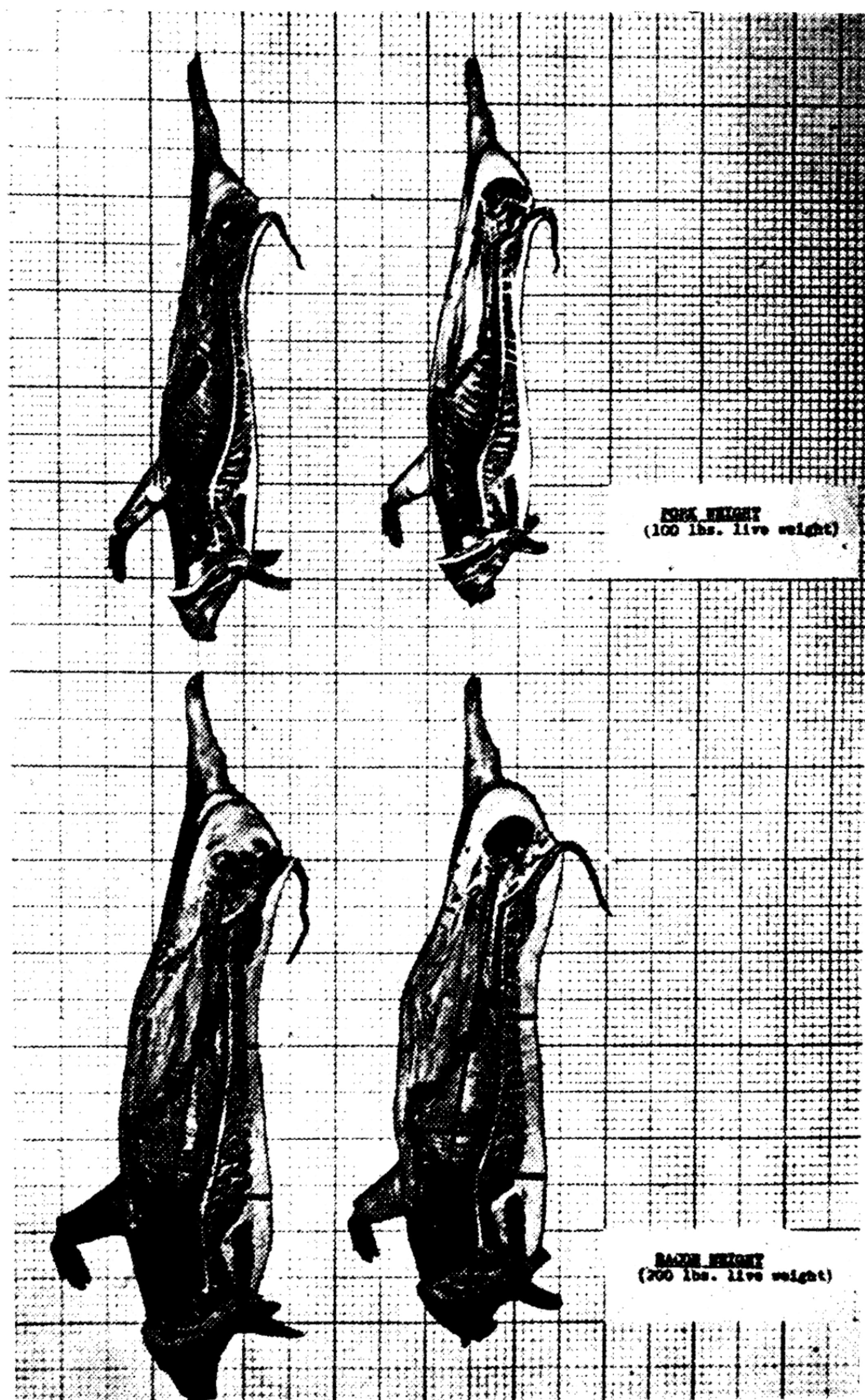


Figure 10.18. Carcasses of Middle White (right) and Large White (left) at 100 lb. live weight for pork (above) and at 200 lb. live weight for bacon (below). Compares with live animals in Figure 10.17. (From Hammond, 1932b, by courtesy of *J. Roy. agric. Soc.*)

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show a definite gradient of increasing growth rate from the extremities towards the trunk (Wilson, 1952). *Figure 10.19* illustrates these changes relative to the size of the different measurements at hatching. The head and the distal bones of the hind limb make the smallest relative gain, while the depth of the thorax and the width of the body make the greatest gain. The difference in the rate of development between the legs and the wings in the fowl is much greater than between the hind limb and fore-limb in the domestic mammals; the wing, having no longer an important function in this species, is much later maturing than the leg. Length growth of bones terminates before growth in thickness (LATIMER, 1927).

The major tissues and body systems measured by weight also exhibit great differential growth from hatching to maturity (Latimer, 1932). *Figure 10.20* illustrates the development of the different tissues and systems relative to the empty live weight from hatching weight of 37 g. to mature weight of 2,600 g. As in mammals the nervous system is earliest maturing, followed by the skeleton and the musculature (muscle and fat). The viscera are earlier maturing than the skeleton while the feathers are later maturing than any of the systems except the muscle and fat. The musculature as a percentage of empty live weight increases from 22% in the newly hatched chick to 48% in the adult, while the nervous tissue decreases from 3.21% at hatching to 0.26% in the adult. The viscera and the skeleton form the highest proportions of the body weight at 100 g. and 500 g., respectively, declining from that stage to form 8.3% and 10.2% of the total in the adult as compared with 21.4% and 14.8% at hatching time.

THE INFLUENCE OF SEX

The influence of sex on the live weight growth and the size of animals is described in Chapter 9. In most species of mammals and birds the male is larger and heavier than the female in adult life, there being only a few exceptions to this rule such as the rabbit (PUNNETT and BAILEY, 1918; ADAMS, 1953) and the guinea-pig (MINOT, 1908; BESSESEN and CARLSEN, 1922-23). As the different parts and tissues of the body do not grow at a uniform rate (*see* pages 433-438) the differences in size between the sexes results in differences in the development of body proportions. ELLIS (1930) divides sexual characters into three groups—primary, that is the organs, other than the gonads, which are concerned in the process of reproduction; secondary, those which are definitely a result of the hormonal activities of the gonads, such as the growth of horns in the male in some breeds of sheep (Merino and Herdwick) and the beard in man which stop developing immediately after the removal of the testis; and tertiary, those which are incidental and appear to be

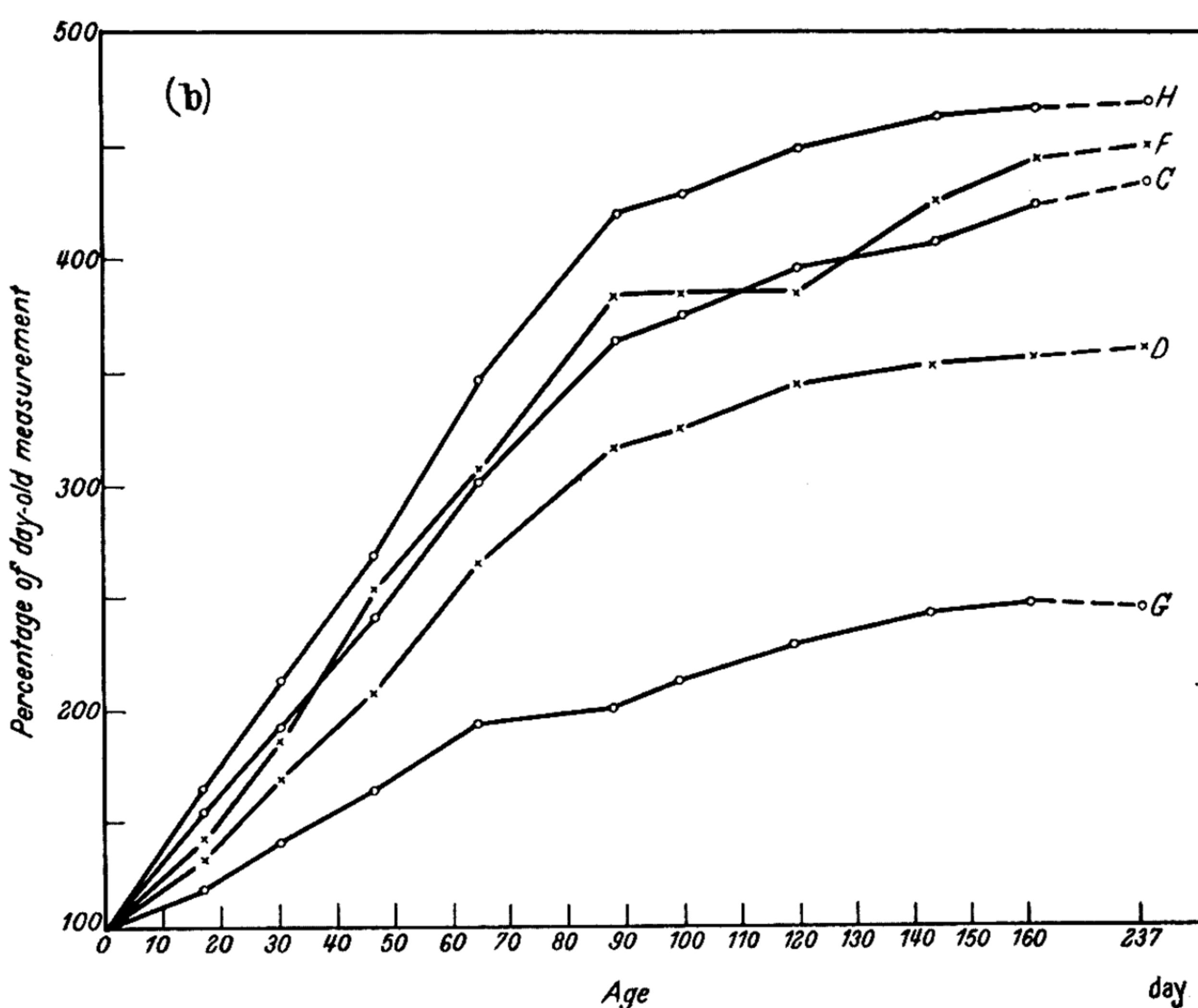
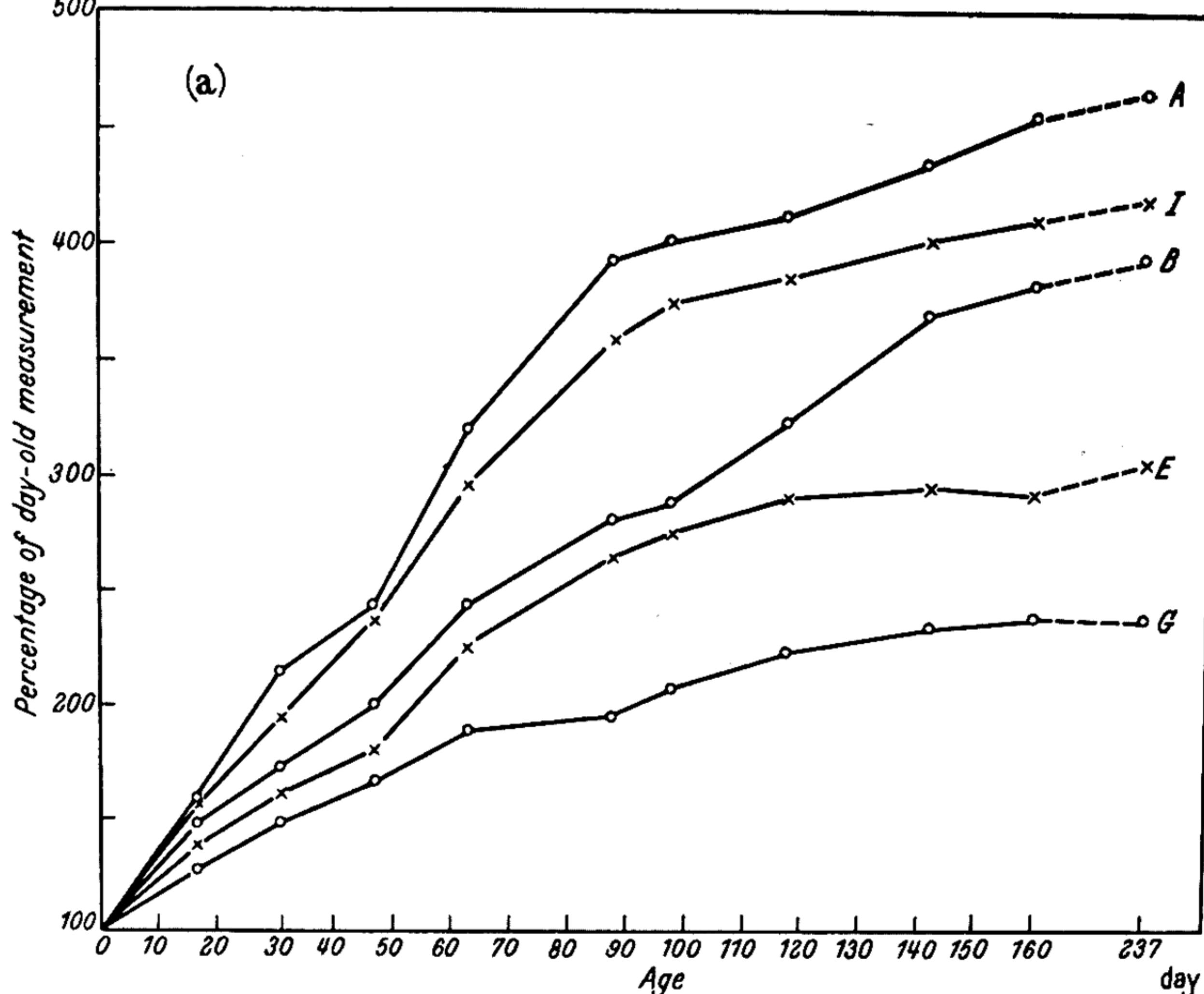


Figure 10.19. (a) and (b). Age changes in external body measurements in pullets relative to the size of the same measurements at hatching. (a) A. Depth of thorax; B. Thickness of tibia-tarsus musculature; E. Length of middle claw; G. Length of head; I. Width across pelvis. (b) C. Length of tibia-tarsus; D. Length of tarso-metatarsus; F. Distance between pubis; G. Length of head; H. Length of mid-wing. (From Wilson, 1952, by courtesy of *J. agric. Sci.*)

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caused indirectly by difference in metabolism during growth rather than by direct stimulus from the gonads.

Castration of either sex reduces sex difference (for literature, *see* Hammond, 1932a). Males castrated at a young age do not develop secondary sexual characters; the bones do not develop to the same extent in thickness although their growth in length is not retarded. They do not attain the broad head and thick and heavy neck and forequarters in general, typical in the entire male (Marshall, 1912; Hammond, 1932a). TANDLER and KELLER (1910) found that spayed

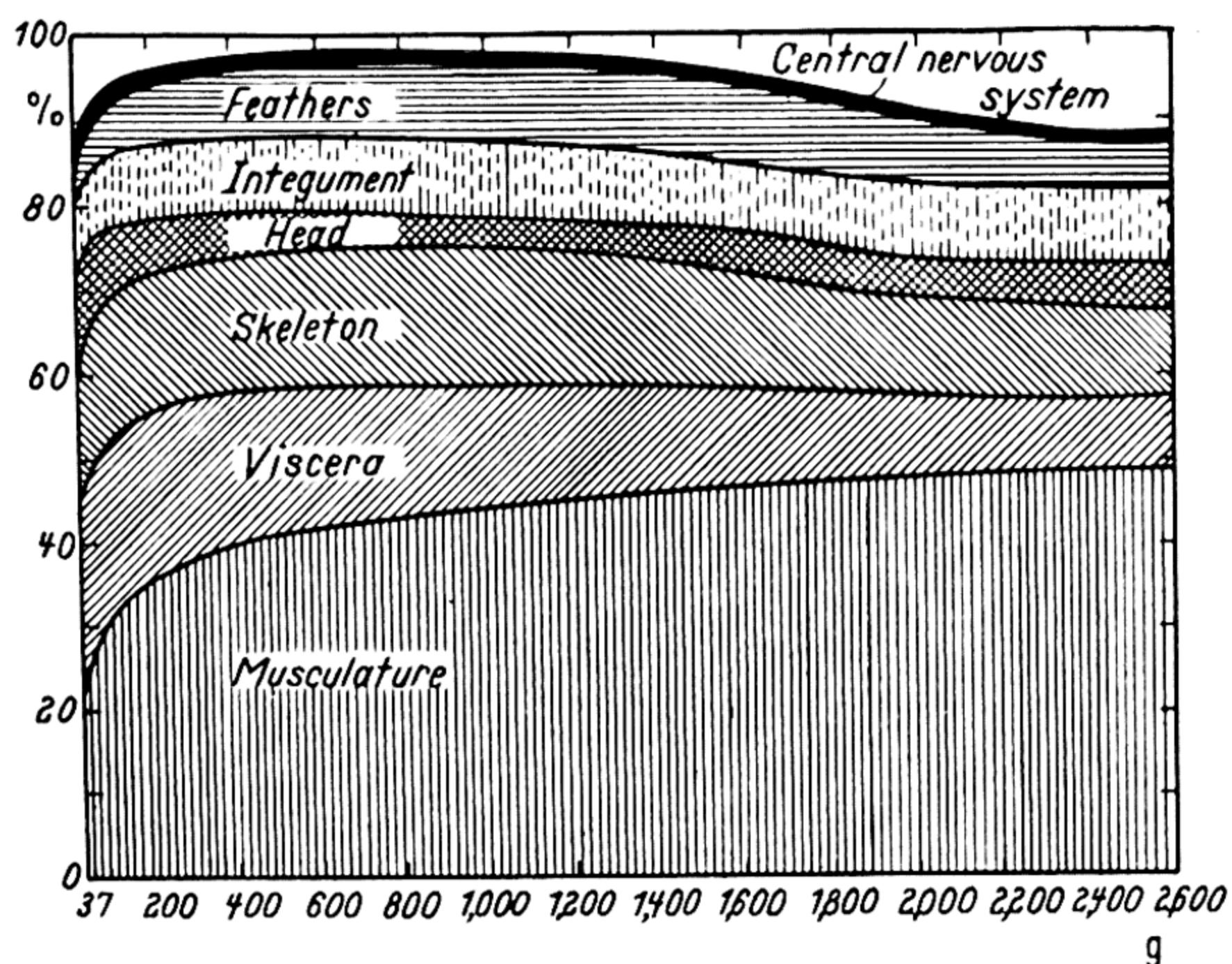


Figure 10.20. Post hatching percentage weight changes in the major body systems with age in White Leghorn chickens. The percentages are shown as ordinates and the body weights as abscissae. The unshaded area at the top represents the "remainder". Note the continuous percentage increase of the musculature. (From Latimer, 1932, by courtesy of *Univ. Kansas. Sci. Bull.*)

heifers lost their feminine characteristics and resembled more the freemartin in their proportions of body length to height, and the ox rather than the normal cow in the shape of their bones.

Although castration of males for meat production has long been and still is universally practised and spaying of females used to be quite commonly performed, very limited exact experimental evidence is available on the comparative effects of castration of both sexes at the same age, and at different ages, on the growth and development of body proportions in farm animals. The excellent work in poultry by FINLAY (1925) and by ZAWADOWSKY (1931) is, however, an exception. In this species, where the normal male is much larger than the normal female at maturity (*see* Chapter 9) these workers found that

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the difference in size between the sexes, unlike secondary sexual characters such as plumage and the size of the comb, is not affected by castration or spaying or by transplantation of the gonads of either sex into the castrates of the opposite sex at hatching (*Figure 9.12*). Whether the difference in size, a tertiary sex character, has a genetical sex linked basis, or is a result of hormonal effects on the somatic tissues operative prior to castration, or is due to some other causes, remains open to speculation until further research work has elucidated this important point.

An optimal level of nutrition is essential for normal development of sexual differences in farm animals (Pálsson and Vergés, 1952) (*see also* page 485), the males being much more severely affected by restricted nutritive supply than the females, probably due to inherent larger size and/or higher metabolic rate of the former as indicated by higher concentration of haemoglobin in the blood of males than females (GÖTZE, 1923; BÖTTGER, 1927; BLACKER, 1926; McCAY, 1931), the castrated male being in an intermediate position in this respect.

Due to this reason sexual differences observed in farm animals reared under varying conditions, or experimental results, where insufficient care has been taken to provide every individual with plentiful food supply, may be grossly misleading.

Sexual differences vary in different species and in different breeds of farm animals (Hammond, 1920, 1932a).

Sheep

Hammond (1932a) and Pálsson and Vergés (1952) have found that sex has great influence on age changes in the body proportions in the sheep. This work has elucidated the fact that females are earlier maturing than the males, *i.e.* the former attaining a more advanced stage of development in early life than the latter, while the males, however, do not only reach greater ultimate size but also attain a higher degree of development at maturity than the females. For example, when comparing ewes and wethers at 9 weeks of age and equal dressed carcass weight of 30 lb. Pálsson and Vergés (1952) found that the ewes had 4.7 per cent higher dressing percentage and had all joints of the carcass, except head and feet, proportionately better developed than the wethers. At this age the earlier maturing tissues, bone and muscle, are lighter in the ewes than in the wethers, while the latest maturing tissue, the fat, is much better developed in the ewes. In the latest maturing fat depot, the subcutaneous fat, the difference between the sexes is still greater than in the earlier maturing intermuscular fat. The earlier maturity of the ewes at this age is furthermore evident from the fact that all skeletal parts, relative to the early maturing cannons, are heavier in the ewes than in the wethers, the difference being greatest in the late maturing trunk bones and least

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in the early maturing bones below the cannons. At 41 weeks, after the animals of both sexes had been continuously growing at as high a rate as their genetic capacity permitted since the 90th day of prenatal life, the situation is completely reversed, the wethers not only being

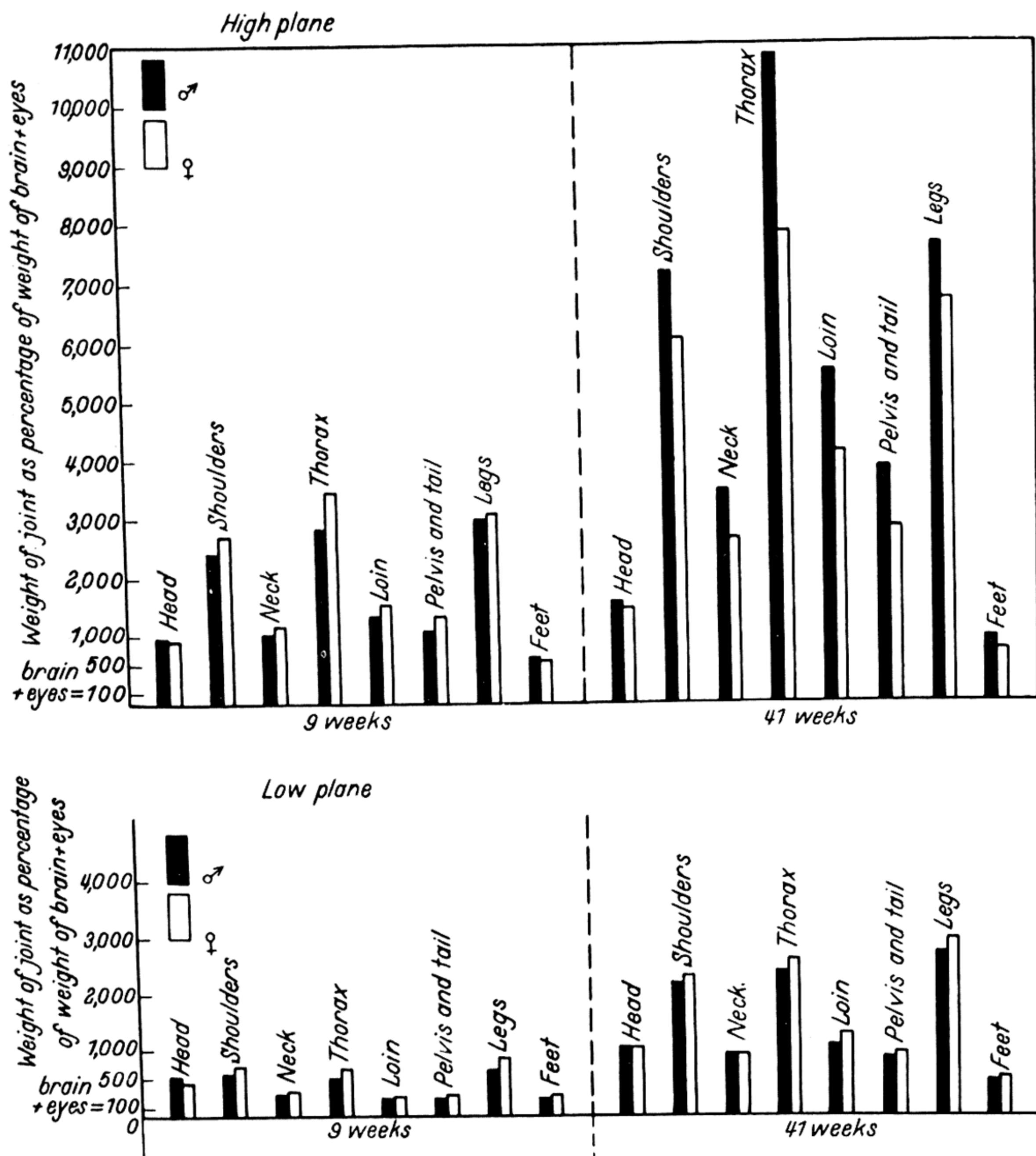


Figure 10.21. Influence of sex on age changes in development of different joints relative to brain + eyes in lambs reared on high and low planes of nutrition, showing earlier maturity and relatively better development of the late maturing joints in the ewes at 9 weeks, whereas at 41 weeks in the high plane group the wethers have all joints relatively better developed than the ewes. In the low plane group the more advanced development of the wethers is completely repressed. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

48 per cent heavier than the ewes, but have also reached a proportionately much higher degree of development of the later maturing parts and tissues of the body. Contrary to the situation at 9 weeks the wethers at 41 weeks have 4.4 per cent higher dressing percentage

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than the ewes and, relative to the weight of the brain-plus-eyes, all joints of the wethers are better developed than in the ewes. The difference is greatest in the late maturing trunk joints and least in the early maturing head and feet, while the neck, legs and shoulders are in an intermediate position (*Figure 10.21*). Furthermore, the wethers have all tissues better developed than the ewes relative to the weight of the brain-plus-eyes in the following order of increasing difference:

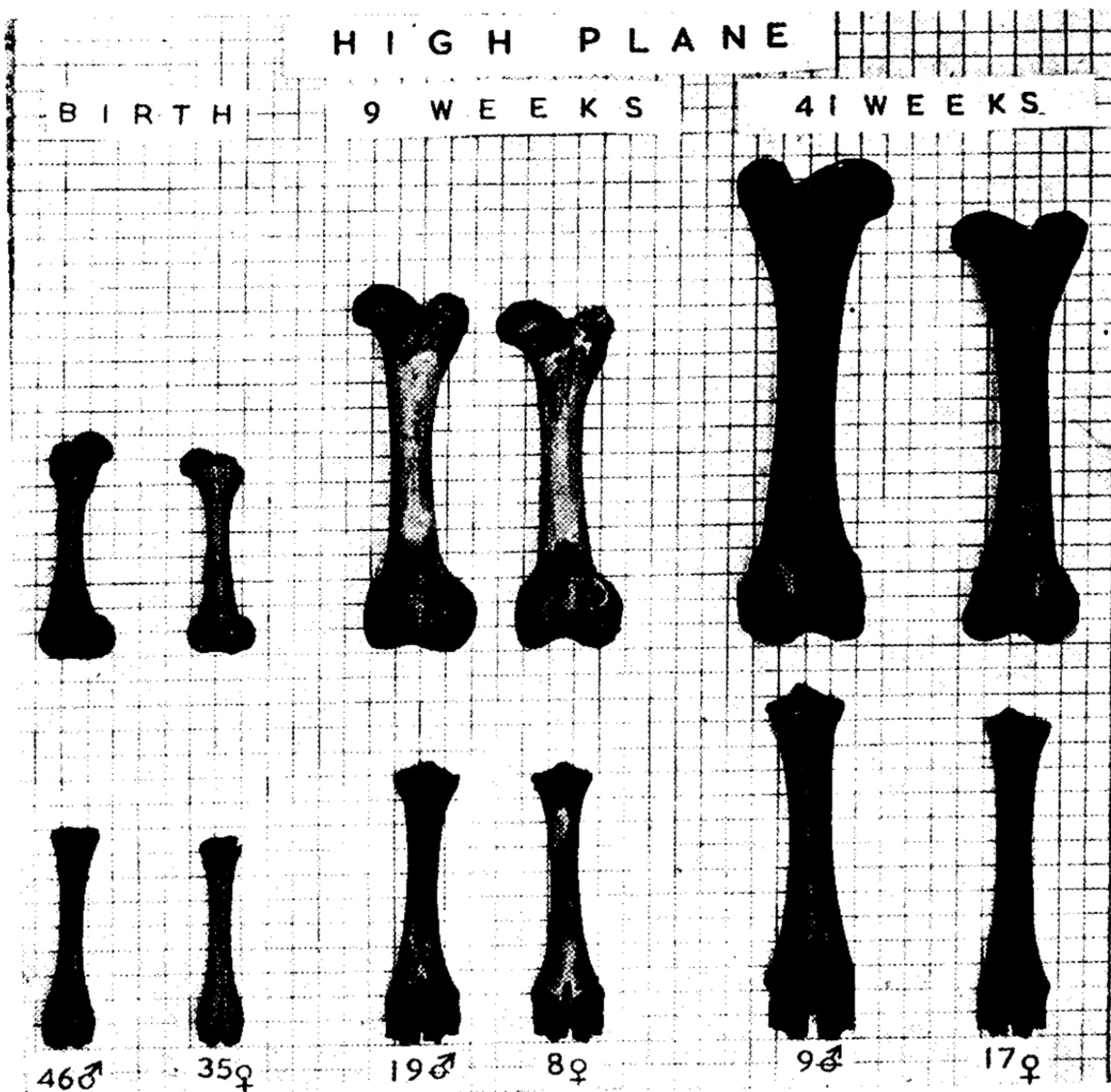


Figure 10.22. Influence of sex on age changes in size and shape of early and late maturing bones, showing increasing sexual differences both in length and thickness with age, and more pronounced in the later maturing femur than the earlier maturing cannon at 41 weeks. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

skeleton, muscle, intermuscular fat and subcutaneous fat. As regards the development of skeletal parts, the picture is also reversed as compared with that at 9 weeks. Relative to the weight of the four cannons the wethers at 41 weeks have all the later maturing skeletal units better developed than the ewes, while there is no difference between

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the sexes in the earlier maturing bones of the hind limb, and the bones of the head are still relatively better developed in the ewes. At 41 weeks even greater sex differences are exhibited in the shape of individual bones than in their weight. At 9 weeks the ewes have slightly shorter but thicker femurs and cannons, while at 41 weeks these bones in the wethers are not only longer but also much thicker, the differences in both dimensions being greater in the later maturing femur than in the earlier maturing cannon (*Figure 10.22*). In the

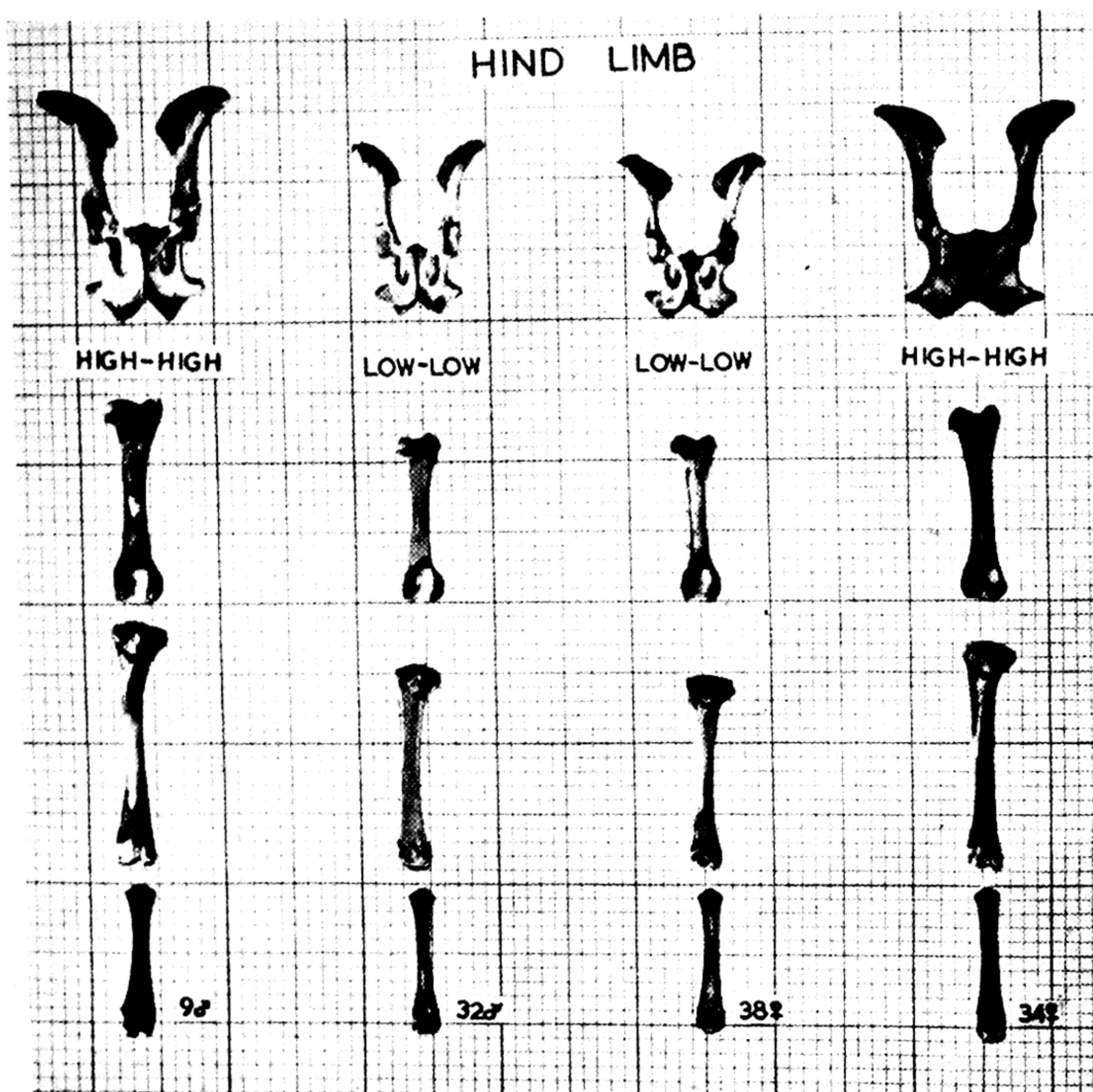


Figure 10.23. Effect of sex and plane of nutrition on size and shape of bones of the hind limb at 41 weeks, showing a distal-proximal gradient of increasing differences due to sex and nutrition. Note the shorter and wider pelvices of the ewes and proportionately greater repressing effects of the low plane nutrition on bone development in the male. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

shape of the pelvis marked sexual difference is observed at 41 weeks; it is much larger and more massive in the wether, but both absolutely and relatively wider in the ewe, particularly in the posterior part (*Figure 10.23* and page 488).

Hammond (1932a), comparing the skeletal development of a ram, wether and ewe at 5 months of age, found that, relative to the

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four cannons, all bones except those of the head and the cervical vertebrae were somewhat better developed in the wether than in the ewe. All skeletal parts in the ram, except the pelvis, were still better developed than in the wether. The difference was greatest in the skull and declined posteriorly along the axial skeleton, indicating greater retarding effects on the anterior than on the posterior part of the body by the removal of the testis (Table 10.2).

That ewes are earlier maturing than wethers and the latter are earlier maturing than rams is also evident from the meat : bone ratio at 5 months, it being highest in the ewe 7.22, intermediate in the wether 6.71 and lowest in the ram, only 6.40. At this age active growth is still taking place in the early maturing skeleton in the ram at the expense of the later maturing tissues, muscle and especially fat, while bone growth in the ewe has slowed down to a very low level so that available nutrients are used for development of the later maturing tissues; the wether is in an intermediate position in this respect. A large scale experiment (PÁLSSON, 1954) comparing entire rams and wethers at equal dressed carcass weight and the same age, 4 months, shows that the wethers are earlier maturing, having higher dressing percentage and better developed fat in the loin region than the rams.

Comparison of skeletal development in rams and ewes at 4 years shows that relative to the weight of the four cannons, all skeletal parts, except the bones below the cannons in the fore-limb, are better developed in the ram. The difference is least pronounced in the bones of the head but is greatest in the cervical vertebrae and decreases backwards to the pelvis and the hind limbs, indicating the relatively better development of the hind than the fore quarters in the ewe (Table 10.2). At this age the rams have both higher muscle : bone and fat : bone ratios than the ewes, again indicating that the former have reached a more advanced stage of development than the latter (Hammond, 1932a).

Cattle

External body measurements and carcass studies indicate that sex affects the conformation of cattle on somewhat similar lines to that described above in the sheep. The bull is born heavier than the heifer and grows at a faster rate in postnatal life (see Chapter 9), with the result that the bull attains a form different to that of the cow. In size and absolute body measurements the steer is in an intermediate position; in weight, however, it is nearer the heifer than the bull (SCHUPPLI, 1911). Relative to the height at withers, which is some 7 per cent less in the cow than in the bull (LYDTIN, 1904), all body measurements in the cow are less well developed than in the bull, the difference being greatest in the circumference of the heart girth and the width and depth of the chest, but least in the length of

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TABLE 10.2
 RELATIVE PROPORTIONS (BY WEIGHT) OF THE DIFFERENT PARTS OF THE SKELETON AS A PERCENTAGE OF THE
 FOUR CANNON BONES IN SUFFOLK SHEEP (from Hammond, 1932a)

Animal	Age	Vertebrae			Fore limbs			Hind limbs		
		Head	Cervical	Thoracic	Lumbar and Sacral	Ribs and Sternum	Pelvis	Above Cannon	Below Cannon	Above Cannon
Ram	5 months	293.5	144.3	140.4	157.5	300.0	106.0	158.2	18.8	164.3
Wether	5 months	229.4	113.5	118.8	138.8	278.0	111.3	149.6	17.7	161.4
Ewe	5 months	252.4	119.5	107.8	134.6	262.3	105.8	142.0	16.8	155.6
Rams (2)	4 years	438.5	211.5	188.1	200.8	430.8	156.3	206.4	18.1	185.5
Ewes (2)	4 years	422.8	169.0	160.1	188.2	399.6	148.4	186.0	18.8	171.4
										16.9

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head and length and width of the pelvis (Lydtin, 1904; Hammond, 1932a). Thus in general the bull exceeds the cow in the development of late maturing characteristics, such as the chest measurements, indicating its higher degree of development. The exception to this is the pelvic region where the cow is approximately as well developed as the bull. The striking difference between the sexes is the great development of the chest and fore quarters in general in the male and the long head and well developed pelvic region in the female. According to Schuppli (1911), quoted by Hammond (1932a), at 6 months old the Murboden steer has much the same absolute and relative body measurements as the heifer, but at $3\frac{1}{2}$ years old it approaches the bull in the height at the withers, but relative to this measurement it has a slightly shallower chest, and considerably narrower chest and hips. Abundant evidence from slaughter tests shows also that the heifer is earlier maturing than the steer. Heifers have shorter bones and fatten to a higher degree than the steer at a relatively young age (MITCHELL *et al*, 1927; TROWBRIDGE and MOFFAT, 1932; BULL *et al*, 1930; HANKINS, 1932; Hirzel, 1939). At light weights, up to 625 lb. live weight, Hankins (1932) and HELSER *et al* (1932) found the fat : muscle ratio to be about the same in steers and heifers. At equal killing weights analyses of the rib cut show that heifers yield smaller percentage of muscle and higher percentage of fat than do steers (Mitchell *et al*, 1927; Bull *et al*, 1930; FOSTER and MILLER, 1933).

The effects of spaying heifers is uncertain. Some workers have found that spayed heifers yield fatter carcasses than entire females and steers (GRAMLICH and THALMAN, 1930), while others have found no advantageous effects on gain or carcass quality from spaying heifers shortly before they were fattened for slaughter (HART *et al*, 1940). The effect of spaying is probably influenced by the physiological age of the animal when the operation is performed and is likely to be less if the heifers are advanced in physiological development when the gonads are removed.

Horses

Although the difference in adult size between the sexes in the horse is much less than in cattle and sheep, both sexes being of the same weight at birth (Isaachsen, 1933; DAWSON *et al*, 1954) and the males not gaining weight at a higher rate than the females until after weaning (Dawson *et al*, 1945), the male, however, proceeds further in the development of the later maturing parts of the body than the female. According to Hering (1925) the stallion is not only larger in almost all body measurements than the mare, but all its measurements except some in the pelvic region are better developed in proportion to the height at the withers.

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From birth to 5 years, all body measurements in the gelding make a greater percentage increase than they do in the mare, the difference being greatest in the depth and the width of the chest and smallest in the circumference of the hind cannon and the knee and in the height at the withers (Isaachsen, 1933).

Pigs

Contrary to what is met with in sheep, cattle and horses, gilts are later maturing than hogs. Carcass measurements show that at similar weights gilts are leaner and have thicker bellies than castrated males (HANSSON and BENGTSON, 1926, 1927; SCHMIDT *et al*, 1931; LACY, 1932; MURRAY, 1934; TUFF and BERGE, 1934; BERGE, 1936; WOODMAN *et al*, 1936; and Hammond and Murray, 1937). At bacon weight measurements of muscle indicate better development of this tissue in gilts than in hogs (Woodman *et al*, 1936). McMEEKAN (1940) using the complete dissection method, compared the development of bone, muscle and fat in castrated males and entire females of the Large White breed, at 200 lb. live weight, in four widely different treatment groups, the pigs within each group being of the same age, while there were wide age differences between the groups. His results showed that in all groups the gilts had heavier skeletons and less fat than the hogs, and muscle was better developed in the gilts in all the groups except the oldest, which had been reared on a low plane of nutrition from birth to slaughter (Table 10.3).

TABLE 10.3

EFFECT OF SEX ON COMPOSITION OF CARCASS IN PIGS AT 200 LB. LIVE WEIGHT (from McMeekan, 1940)

Plane of Nutrition	H-H		H-L		L-H		L-L	
	Weight g.	Prop.	Weight g.	Prop.	Weight g.	Prop.	Weight g.	Prop.
Total skeleton	♂ 6,930	100	7,159	100	5,978	100	7,888	100
	♀ 7,186	104	7,890	110	6,819	114	8,141	103
Total muscle	♂ 25,059	100	27,434	100	22,669	100	31,782	100
	♀ 27,667	110	32,676	119	25,407	112	31,761	100
Total fat	♂ 25,590	100	25,242	100	32,177	100	18,476	100
	♀ 24,502	96	19,469	77	26,231	81	17,095	92

Gilts give carcasses of higher quality than hogs, because at present the demand is for a high muscle : fat ratio in both pork and bacon, and a thick belly is desirable in a bacon carcass. Castration in either sex results in increased development of back fat and entire gilts appear to accumulate more fat than boars (Hammond and Murray,

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1937). Castration of the male appears to have greater effects in increasing early maturity of the body tissues in general in the pig than in sheep and cattle. This may be due to differences in physiological age when the operation is performed, pigs being physiologically younger than lambs or calves at castration time. Further research work is necessary to elucidate this point.

Poultry

The cock is larger and later maturing than the hen. No sex differences are observed at hatching but shortly afterwards, however, the male begins to grow at a faster rate than the female. This difference is reflected both in weight and body proportions (Mitchell *et al*, 1931; Wilson, 1952). Sex differences in the age changes in external body measurements, whether compared at equal age or at equal body weight, show that most of the measurements increase both actually and relatively at a higher rate in the male than in the female. At similar live weight, therefore, the pullets are more compact than the cockerels. Wilson (1952) found greatest sexual dimorphism in the length of the wing, this part increasing much more in the cock than in the hen after hatching. This he believes to be due to function, as a male uses the wings in courtship. According to Mitchell *et al* (1931) pullets when compared with cockerels at equal body weights in the later stages of growth, have two measurements, the depth at the rear end of the keel and the width at hips, better developed than the cockerels. At 4 lb. body weight the difference in favour of the cockerel was greatest in the length of the shank and the drumstick. The changes in proportion of muscle and fat to bone take place more rapidly in pullets than in cockerels, so that pullets are as a rule ready for slaughter at an earlier age than cockerels. Comparing sex differences in age changes in body proportions, by expressing the weight of each part in the pullet as a percentage of the same part in the cockerel at equal body weight, Mitchell *et al* (1931) found that the torso is relatively better developed in the pullets, while the legs above the hocks and the neck are better developed in the cockerels, these differences increasing with age. At 2 lb. body weight they found that the bone in the dressed carcass in pullets is 95 per cent and the flesh 108 per cent of the same tissues in the cockerel and at 4 lb. body weight the corresponding figures are 80 per cent for the bone and 110 per cent for the flesh. Pullets give more breast meat as a percentage of the dressed carcass than cockerels of the same age and weight, the difference increasing from 0.9% at $2\frac{1}{2}$ lb. to 4% at $3\frac{1}{2}$ lb. and then decreasing to 0.8% at 4 lb. (HALNAN and FERMORE, 1937). Pullets have greater capacity for fat storage than cockerels and this difference becomes most marked at the onset of sexual maturity (HALNAN and CRUICKSHANK, 1933). The bone development is

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greater in cockerels than pullets both actually and proportionately (HALNAN, 1936).

Although castration does not directly affect ultimate size of poultry (see page 465 and *Figure 9.12*), caponizing, however, increases the rate of development, thus encouraging quicker fattening and greater deposits of fat which may result in actually greater weight of the capon compared with the cockerel (HOROWITZOWA, 1931).

THE EFFECTS OF PLANE OF NUTRITION

Age changes in body proportions as well as in the development of the different tissues and organs of an animal can be controlled by the plane of nutrition during the period of growth. McMeekan (1940, 1941) and POMEROY (1941) in the pig, Vergés (1939a, 1939b), WALLACE (1944, 1945, 1948) and Pálsson and Vergés (1952) in the sheep, and Wilson (1952) in poultry have found that restricted nutrition at any age from the late foetal stage to maturity does not merely retard growth in general but that it affects the different regions of the body, the different tissues and the various organs differentially so that an undernourished animal of certain weight differs vastly in form and composition from another younger individual of the same breed and weight. They have proved beyond doubt that the animal's form can be controlled at will by changing the plane of nutrition at different stages during growth. This can be done to a varying degree within the wide limits which are imposed on the one hand by the genetic capacity of the animal for development and on the other hand by under-nutrition which may result in death. The results of these workers showing how limited nutrition supply affects the different species will be referred to below (page 447). In general their findings are that (1) Severe under-nutrition of the dam has no retarding effects on the development of the foetus until the later stages of foetal life; (2) During late foetal life to maturity any part, organ or tissue of the animal's body is proportionately most retarded in development by restricted nutrition at the age when it has its highest natural growth intensity; (3) Restricted nutrition during any age interval, from the late foetal stage until growth ceases, has an increasing retarding effect on the different tissues and parts of the animal's body in the direct order of their maturity, *i.e.* the earliest maturing parts or tissues are least and the latest maturing ones are most affected; (4) When an animal is kept on a sub-maintenance ration the different tissues and body regions are utilized for the supply of energy and protein required for the maintenance of life in the reverse order of their maturity, *i.e.* fat is first utilized, followed by muscle and then by bone; these tissues are first depleted in the latest maturing body regions such as the loin and pelvis. Before the very early maturing nervous tissue is utilized for energy supply, death will most likely occur; (5) Any part,

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organ or tissue of a growing animal, which has been retarded in development by restricted nutrition, exhibits great recuperative capacity, if the animal is changed on to a high level of nutrition. In many cases, provided the animal has not been subjected to too severe under-nutrition for a long period, the under-developed organs or tissues may completely recover from the retarding effects sustained earlier on.

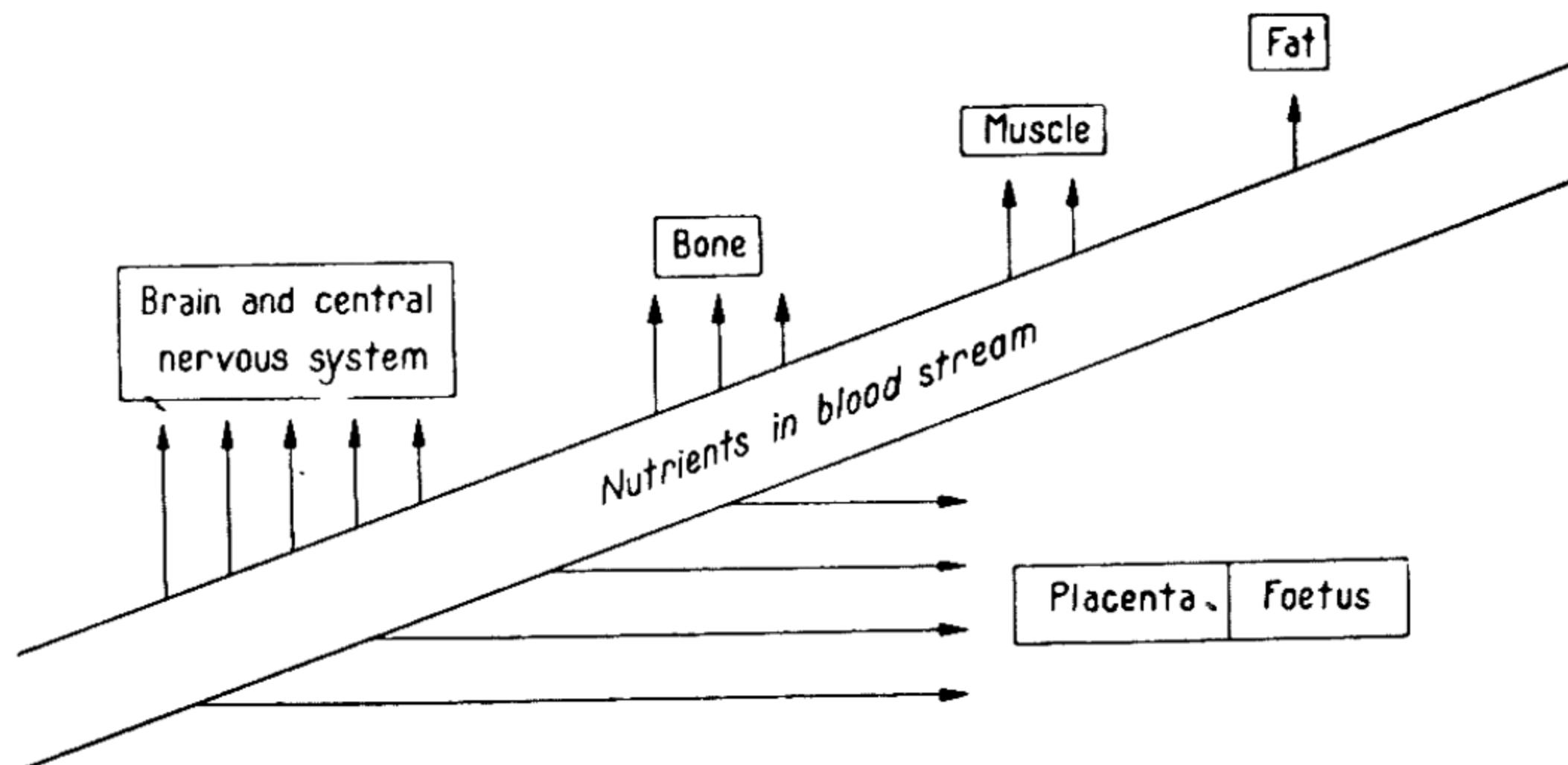


Figure 10.24. Diagram showing how the different tissues of the body compete for nutrients in the blood stream. Priority of supply varies in different tissues (denoted by arrows) according to their order of development and metabolic rate. When the plane of nutrition is reduced (1 arrow taken from each) fat growth ceases but brain, bone and muscle continue to grow at a slower rate. When the plane of nutrition is reduced still further (2 arrows removed) muscle ceases to grow, but fat is now removed to the blood stream (arrow reversed) to assist in the growth of brain and bone, which still continue to grow but at a slower rate. (From Hammond, 1944, by courtesy of *Proc. Nutr. Soc.*)

The interplay between nutrition and the development of the different organs, parts and tissues of the body is explained by HAMMOND (1944) in *The Theory of Partition of Nutrients According to Metabolic Rate* and illustrated schematically (*Figure 10.24*). CHILD (1920) first showed that the partition of incoming nutrients is determined by the metabolic rate of the tissues concerned, the tissue, part or organ of highest metabolic rate thus having priority in supply over tissues, parts and organs with a lower metabolic rate. In the diagram (*Figure 10.24*) the number of arrows denotes the metabolic rate of the tissues and the placenta. When the nutritive supply is plentiful all tissues of a growing animal, and/or of a pregnant female, receive sufficient nutrition for maintenance as well as for normal growth. On the other hand, when the supply of nutrients in the bloodstream is limited one arrow may be deducted from each tissue and growth of fat is then completely stopped, whereas growth of other earlier maturing tissues continues but at a slower rate. By further reducing

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the nutritive supply the direction of the arrow for fat is reversed and another arrow deducted from each of the other tissues and the placenta; this illustrates that the early maturing brain, bone and foetus still continue to grow while muscle ceases to grow and fat is lost to supply the animal with energy. At a still lower level of nutrition bone growth ceases and both muscle and fat are broken down for maintenance and growth of the foetus and the central nervous system, the most vital organ. Further reduction in the supply of nutrients will result in the death of the foetus and finally of the animal itself.

Sheep

During the first three months of pregnancy a low plane of nutrition of the ewe has no retarding effects on the development of the foetus, while during the last two months of foetal life the development of the lamb is greatly affected by the level of nutrition of the ewe, restricted nutrition at that stage having much greater retarding effects on the development of twins and triplets than of singles (Wallace, 1948; Vergés, 1939a, 1939b; *see also* page 468). Thus during the early stages of pregnancy the placenta and the foetus too have high priority for the available nutrients in the blood stream of the dam, while in the later stages there is a greater competition between the maternal and foetal tissues (*Figure 10.24*). Wallace (1948) found that twin foetuses from ewes, which lost considerably in live weight during the last two months of pregnancy, gained only 46.7 per cent of the body weight of twin foetuses from ewes which were well fed during this period. The different foetal organs and tissues were differentially affected by the restricted maternal nutrition; the organs as a whole were slightly more affected than the carcass. Of the major body tissues, the brain and spinal cord were least affected followed by bone and by flesh. The increments in the nervous tissue during the last 53 days of pregnancy in the Low plane foetuses were 84% of the increment in the High plane ones; the corresponding figures for bone and flesh were only 55% and 43% respectively. Pálsson and Vergés (1952) have shown how the plane of nutrition of lambs during the late foetal and the postnatal period of growth affects body conformation as well as the development of the various organs, parts and tissues of the body. They approached the subject from two different angles: (1) By comparing the development of Suffolk \times Border Leicester-Cheviot half-brother-sister lambs of balanced sexes, which were reared on two quantitatively vastly different, High and Low, planes of nutrition from the 90th day of foetal life to 41 weeks. Comparisons were made *at equal age* but at different weights at three ages, birth, 9 weeks, and 41 weeks; (2) By comparing the development of four groups of 8 lambs each of balanced sexes of the same breed, killed *at the same dressed carcass weight* of 30 lb. but at three different ages,

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9 weeks, 15 weeks, and 41 weeks. These four groups were reared from the 90th day of foetal life to slaughter so as to follow four widely different predetermined growth curves, *viz.*:

- (a) On a High plane throughout, killed at 9 weeks, referred to as the High-High group.
- (b) On a High plane up to six weeks, followed by a Low plane until killed at 15 weeks, referred to as the High-Low group.
- (c) On a Low plane up to six weeks, followed by a High plane until killed at 15 weeks, referred to as the Low-High group.
- (d) On a Low plane throughout, killed at 41 weeks, referred to as the Low-Low group.

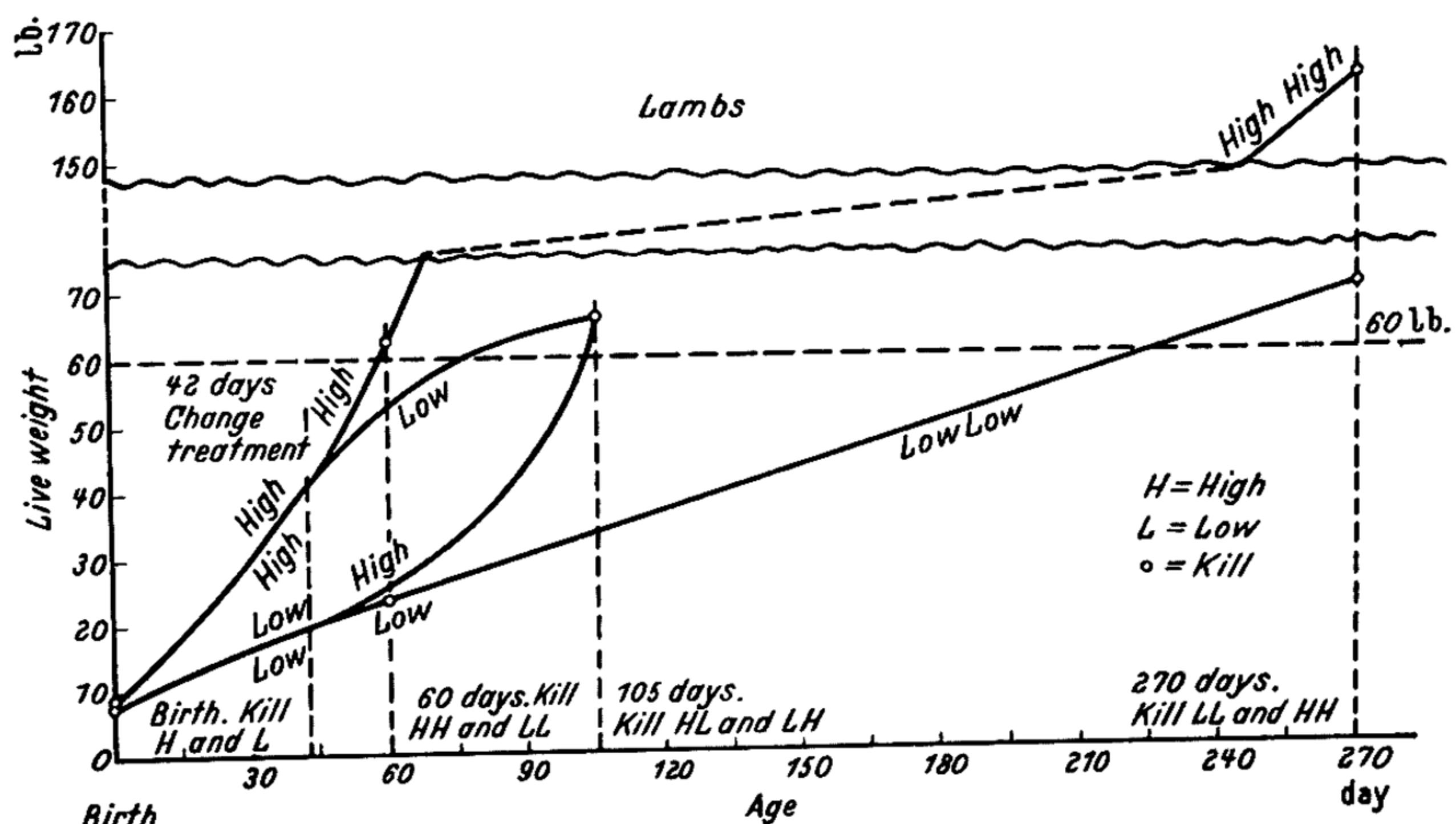
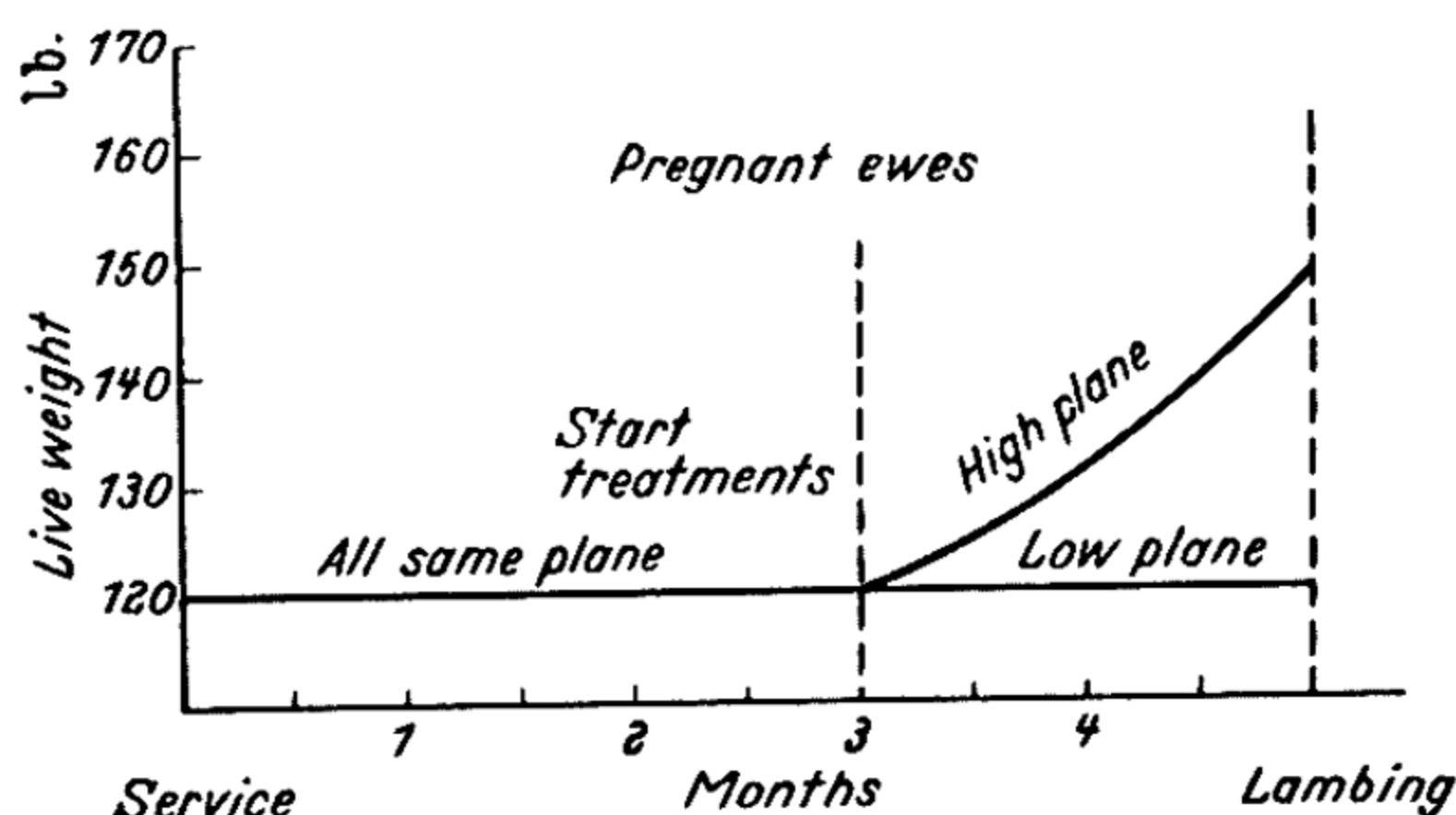


Figure 10.25. Growth curves controlled by feeding on different planes of nutrition. *Top*—Ewes during pregnancy. *Bottom*—Lambs from birth to slaughter. The effects of this on the proportions of the carcass, organs and tissues are shown in Figures 10.26 to 10.44. (From Vergés, 1939a, by courtesy of Suffolk Sheep Society Year Book.)

Figure 10.25 illustrates the plan of the experiment, the extent of the treatment differences of the High and Low plane ewes during the last two months of pregnancy and the predetermined growth curves of the lambs. (1) *In the age series*, Pálsson and Vergés (1952) compared the relative effects of the two treatments on the development of the different organs, parts and tissues of the body by expressing the weight of each organ, part or tissue in the High plane groups as a percentage of the same organ, part or tissue, in the Low plane group at the same age. The two quantitatively different planes of nutrition not only produce animals of greatly different weights at the same age, but also of vastly different conformation and composition. In general, the results were in agreement with the statement above (page 475) that any organ, part or tissue is proportionately more affected by restricted nutritive supply at the age of its highest growth intensity than at any other age, and that the low plane of nutrition has increasing retarding effects on the development of the different anatomical units and tissues in the direct order of their maturity.

The brain, the earliest maturing organ (see page 453) is at all stages less retarded in development by the Low plane of nutrition than any other organ or part of the body; at 41 weeks its weight is only 5 per cent more in the High plane lambs than in the Low plane ones, though the corresponding live weight difference between these groups amounted to 59 per cent. The actual and relative difference in brain weight in grammes and per cent was higher at birth than at 41 weeks; this indicates that in prenatal life, while the growth intensity of the brain is highest, its development is slightly retarded by restricted nutritive supply in spite of its very high priority for the available nutrients. In postnatal life, however, its development is not affected for it is even able to make up for some of the retardation sustained earlier on in spite of severe and prolonged under-nutrition, because of its relatively low growth intensity at that stage and its high priority for the available nutrients at any age.

The various internal organs are differentially affected by a Low plane of nutrition. The magnitude of the differential effects on the individual organs and how they change with age is illustrated in *Figure 10.26*. In prenatal life the thymus glands, gall bladder, kidney fat, spleen, oesophagus and abomasum are most affected. The alimentary tract as a whole is more affected than the thoracic organs by the restricted nutrition. At the end of each age interval the earlier maturing organs are as a rule less retarded in development than the later maturing ones by the Low plane of nutrition. There are, however, a few exceptions where the development of an organ appears to depend primarily on its function at some age; for example, the alimentary tract, which is later maturing than the thoracic organs, is less depressed by a Low level of nutrition in postnatal life, the

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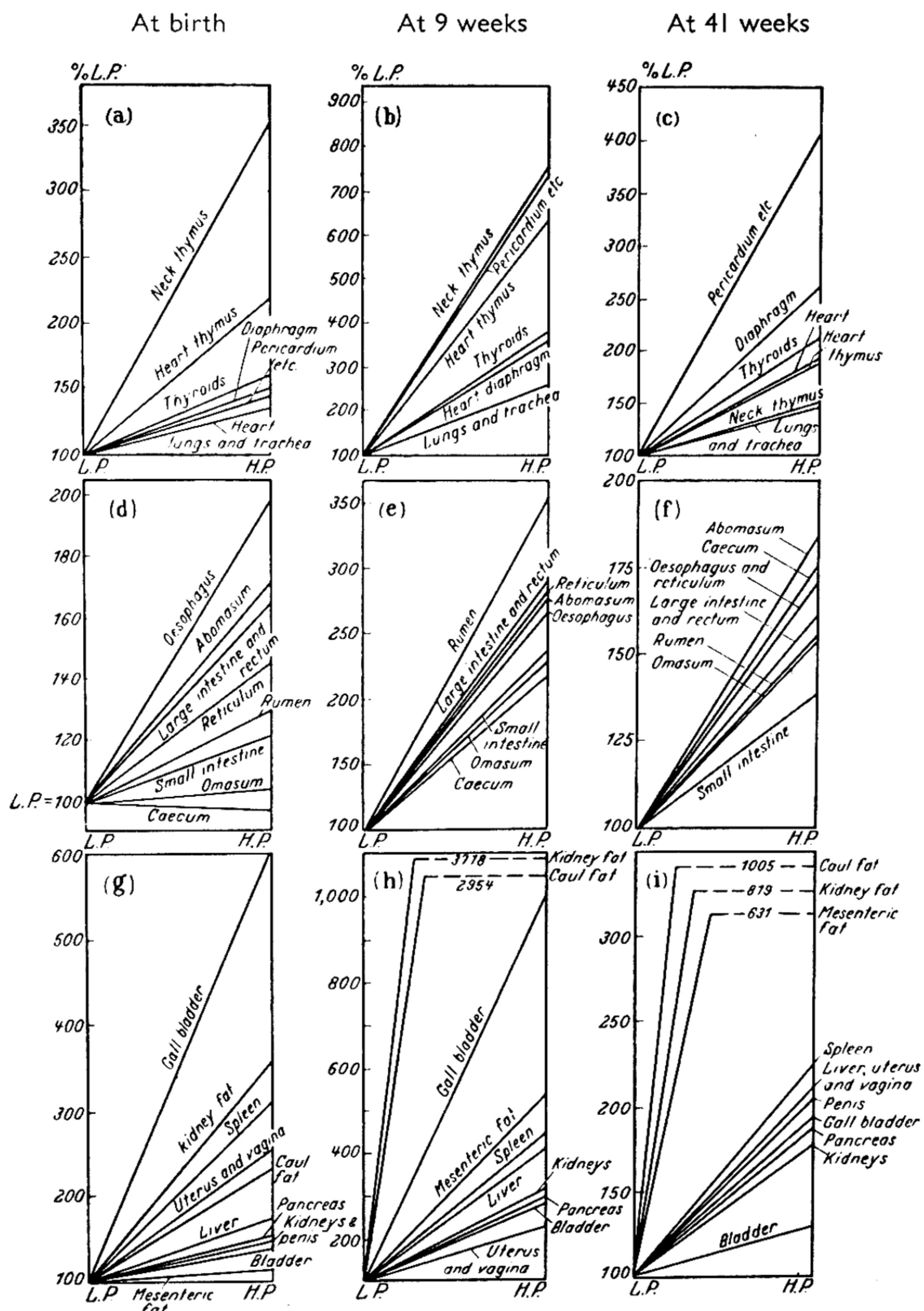


Figure 10.26. The effect of plane of nutrition on development of organs in lambs with age. Weight of each organ in the High plane lambs expressed as percentage of the weight of the same organ in the Low plane ones at each age. Compare with *Figure 10.10* and note greater repressing effect of the low plane feeding on organs of high growth intensity at each stage and the lesser effect on organs of great functional importance as the heart, lungs and alimentary tract. (a) (b) and (c) thoracic organs; (d) (e) (f) organs of alimentary tract; (g) (h) (i) other organs and loose fat. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

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development of the alimentary tract being of great functional importance in the Low plane animals to cope with the digestion of large quantities of fibrous roughage of low feeding value.

How restricted nutrition affects carcass conformation up to 9 weeks and 41 weeks respectively is illustrated in *Figures 10.27* and *10.28*. Whereas a High plane of nutrition gives a short-legged, blocky carcass

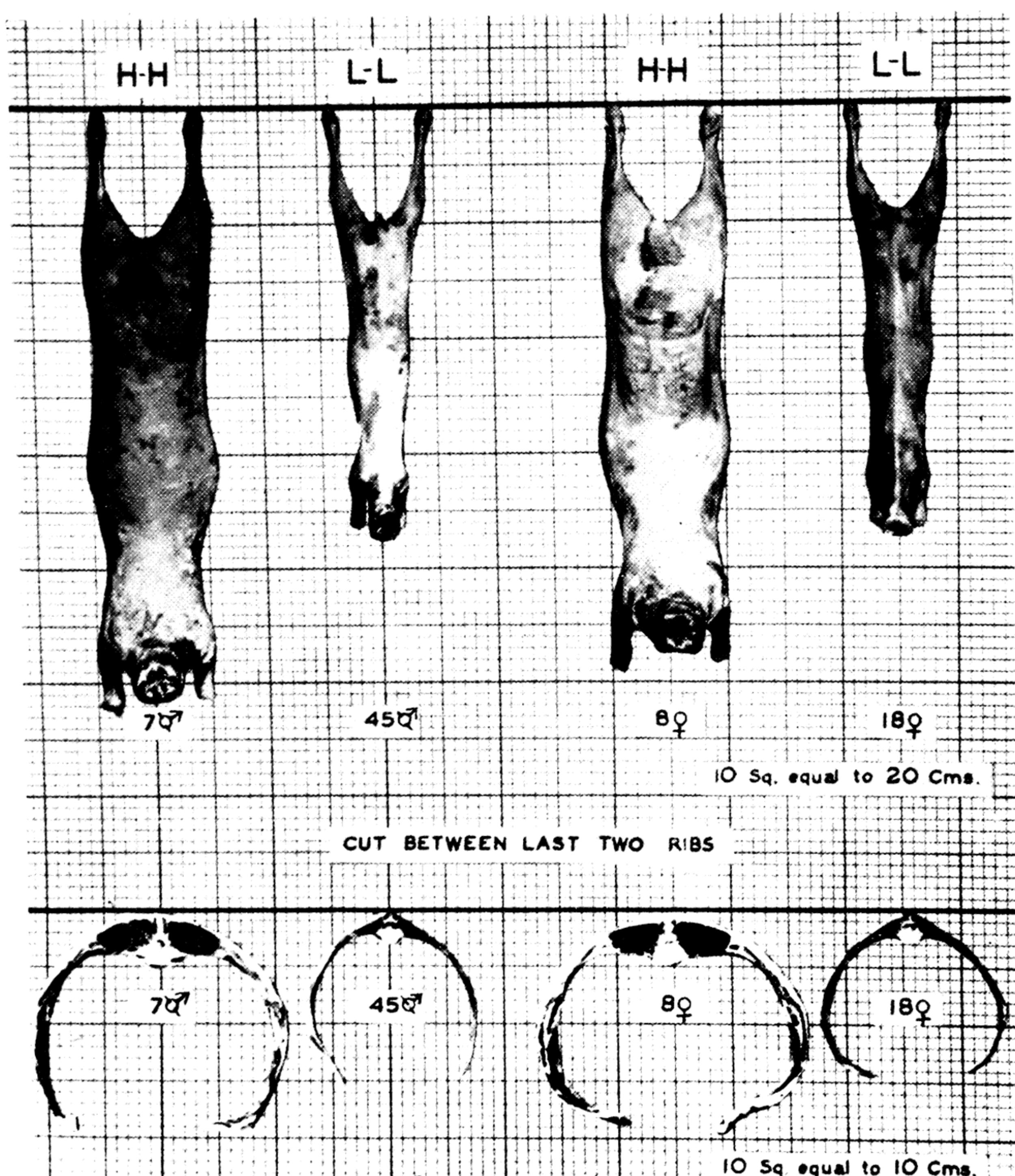


Figure 10.27. Effect of the plane of nutrition on carcass proportions in lambs at 9 weeks, showing proportionately much greater retarding effects of a low plane feeding on the development of muscle and fat and on the width of the body than on the length of the limbs. HH = high plane nutrition; LL = low plane nutrition. *Left*—Wethers; *Right*—Ewes. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

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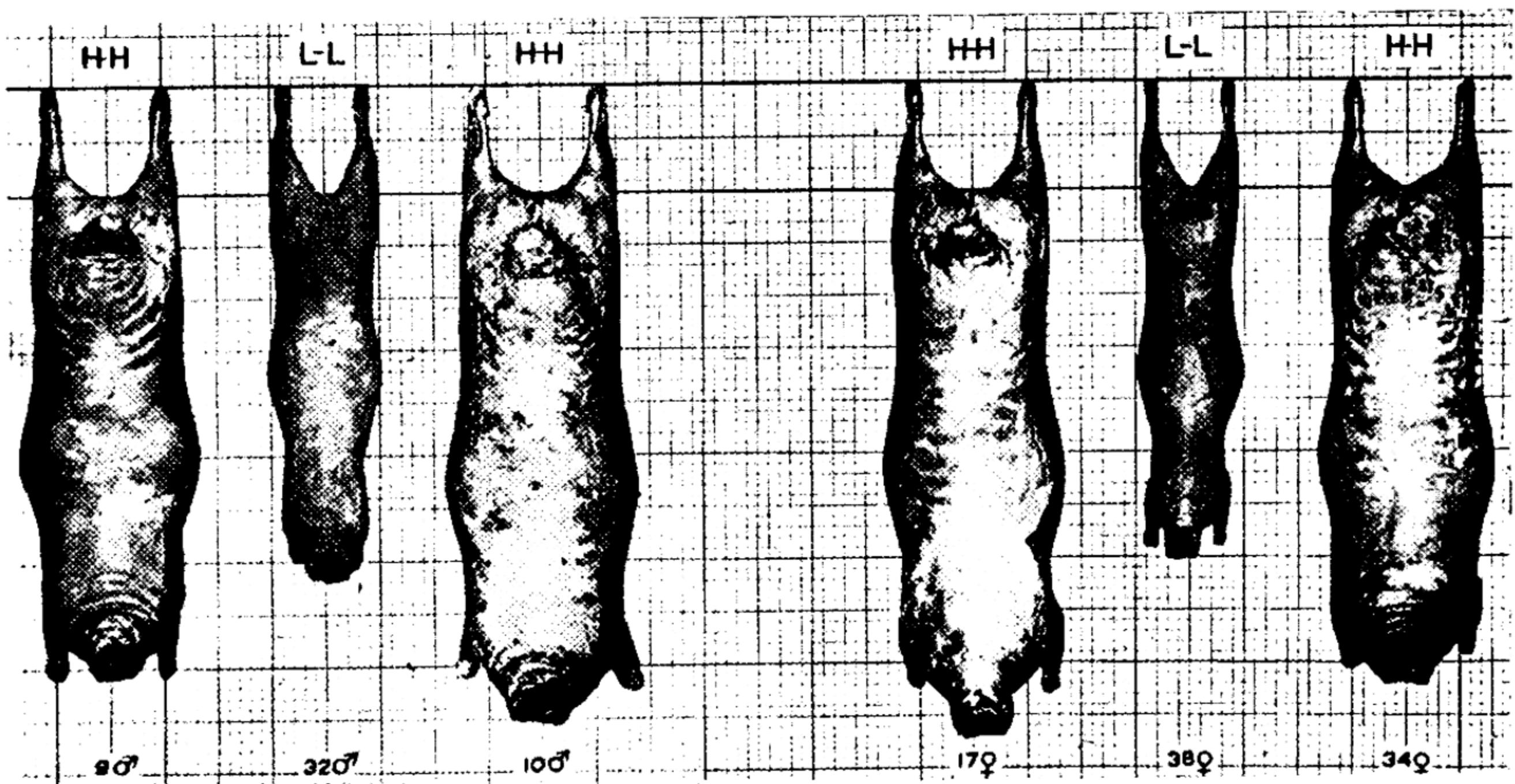


Figure 10.28. Effect of the plane of nutrition on carcass proportions in lambs at 41 weeks, showing proportionately much greater retarding effect of low plane feeding on development of body width than body length and on body length than on leg length. HH = high plane nutrition; LL = low plane nutrition. *Left*—Wethers; *Right*—Ewes. All photographed to the same leg length to show differences in proportions as distinct from differences in size. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

with a well developed trunk and excellent cover of subcutaneous fat at both ages, typical of an early maturing improved breed, the Low plane carcasses have relatively long legs and necks, are narrow and lean, lack finish and especially the development of flesh in the hind quarters and the loin region. At 9 weeks the Low plane carcasses resemble more those of new-born lambs and at 41 weeks those of an unimproved late maturing breed than the High plane carcasses of the same age.

Restricted nutrition in foetal life has less differential effects on the weight of the different joints of the carcass than in postnatal life (*Figure 10.29*, and Wallace, 1948), probably due to the relatively late maturity of all joints of the carcass as compared with the organs and offal parts. In the Low plane lambs at birth, the head, neck and feet are best and the legs least developed in proportion to the same parts in the High plane lambs. In postnatal life the various joints are affected by a Low plane of nutrition to a very different extent, depending on their growth intensity at each age interval, but in general they are retarded in development in reverse order of their early maturity; the early maturing head, feet and legs are least, and the late maturing loin, pelvis, tail and thorax are most affected (*Figure 10.29*). The major tissues of the carcass are differentially affected by a Low plane of nutrition in reverse order of their early

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maturity, or in their direct order of increasing growth intensity with age. The brain is least retarded and is followed in increasing order by the skeleton, muscle and fat. The different fat depots of the carcass are approximately equally affected in prenatal life, but in postnatal life the subcutaneous fat is most affected followed in a

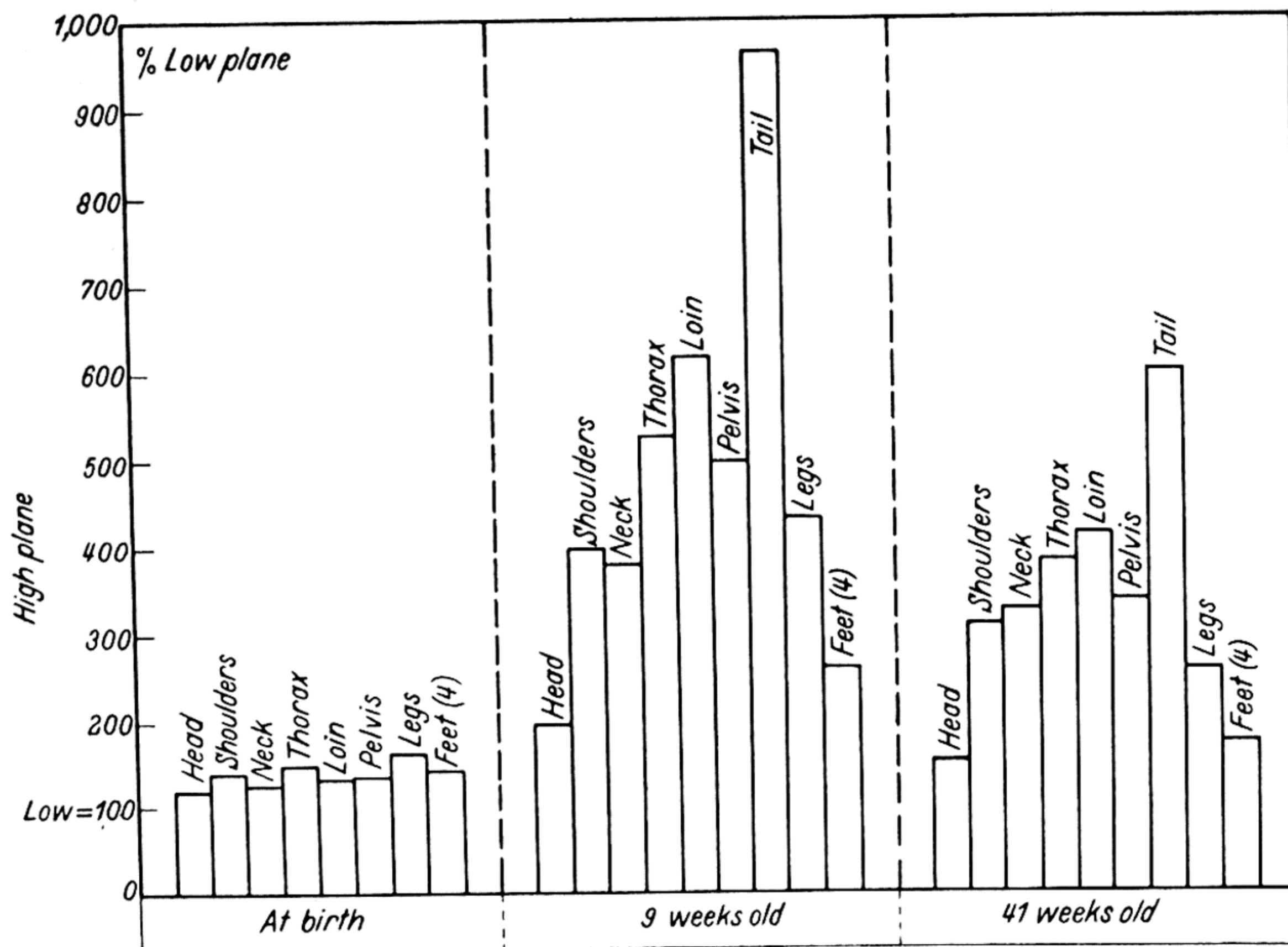


Figure 10.29. Effect of plane of nutrition on development of different joints in lambs with age. Weight of each joint in the High Plane lambs shown as percentage of the weight of the same joint in the Low Plane lambs. Note less differential effect in prenatal than postnatal life. Compare with *Figure 10.11* and note the gradient of increasing retarding effects of the low plane feeding on the development of the joints in the direct order of their postnatal growth intensity. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

decreasing order by the kidney fat and the intermuscular fat (*Figures 10.12* and *10.30*). Restricted nutrition produces also marked differential effects on the relative development of the different anatomical units within each of the major tissues of the body, bone, muscle and fat. As regards the skeleton, individual bones or skeletal parts are retarded in development in direct relation to their growth intensity at each age interval (*Figures 10.13*, *10.31* and *10.32*). At birth the bones with the highest growth intensity in foetal life, like the short bones of the limbs (*Figures 10.13* and *10.32*) are relatively more severely penalized by the restricted nutrition in prenatal life than other bones in the skeleton, which do not exhibit marked differential effects at this age. At later ages the development of the later maturing bones is much more affected. At 41 weeks, for example, the bones of the

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fore-limb are retarded in development by the Low plane of nutrition exactly in the reverse order of their maturity. The carpal are least affected, followed by the cannon, the bones below the cannon, the

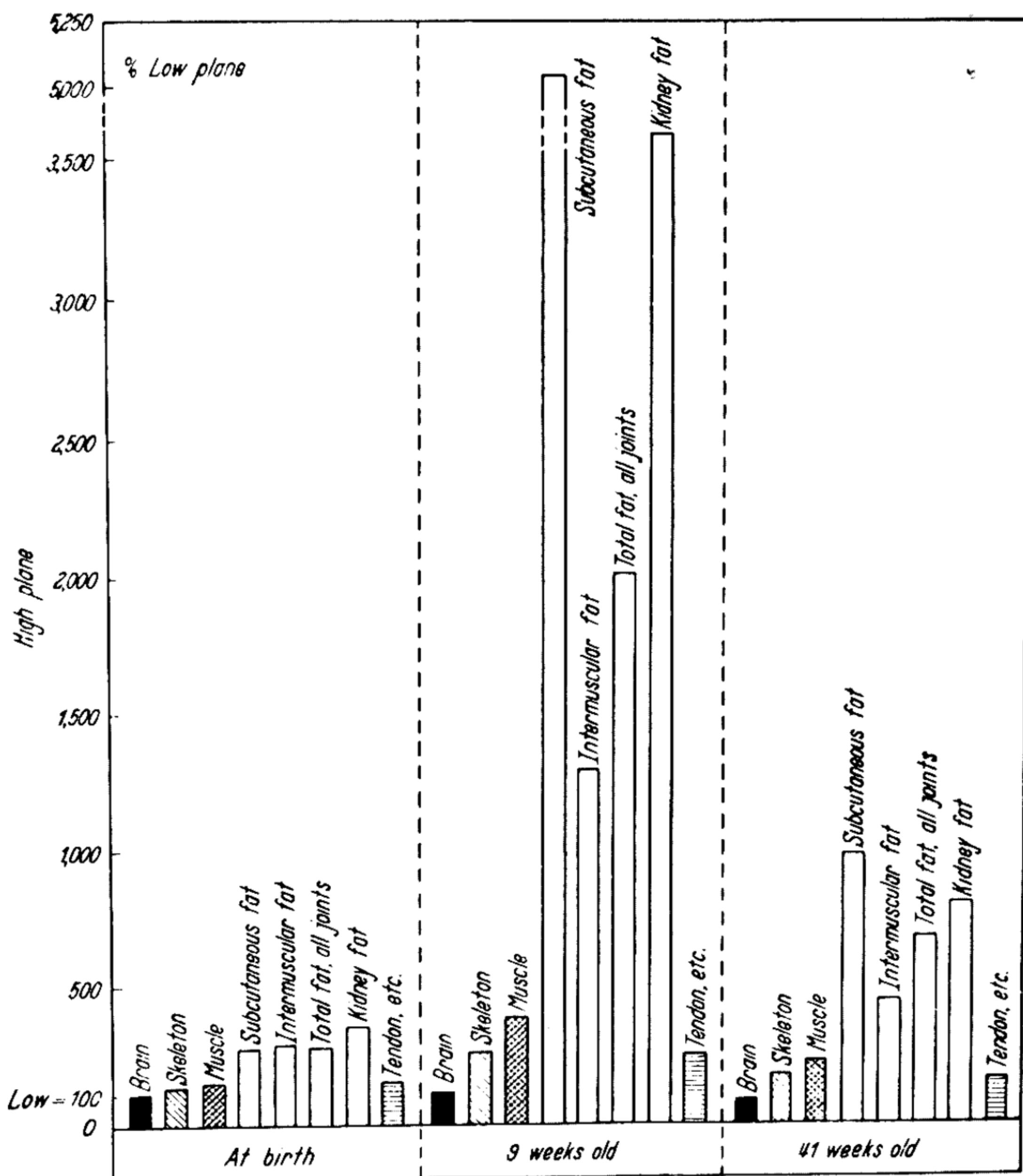


Figure 10.30. Effect of plane of nutrition on development of the major tissues of lamb carcasses plus head and feet with age, showing a gradient of increasing retarding effects of the low plane feeding in a direct order of increasing postnatal growth intensity of the tissues. Compare with *Figure 10.12*. Weight of each tissue in High Plane lambs shown as percentage of the same tissue in Low Plane ones at each age. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

radius-ulna, humerus and the scapula, which is by far the most affected of the limb bones both at 9 and 41 weeks (compare *Figures 10.13* and *10.32*). The plane of nutrition affects the form of individual bones in a comparable way to its effect on their weight. The later developing growth in thickness is retarded by poor nutrition to a much greater extent than the earlier developing length growth in postnatal life. In foetal life, however, the length growth of the early

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maturing cannon is more affected than its later maturing growth in thickness, the latter having very low growth intensity in foetal life as compared with length growth (*Figure 10.33*). Persistent under-nutrition from the 90th day of foetal life to 41 weeks old inflicts so great a differential effect on the form of the early maturing metacarpals, that these bones in the Low plane lambs at 41 weeks resemble those of semi-wild or unimproved late maturing breeds, being very

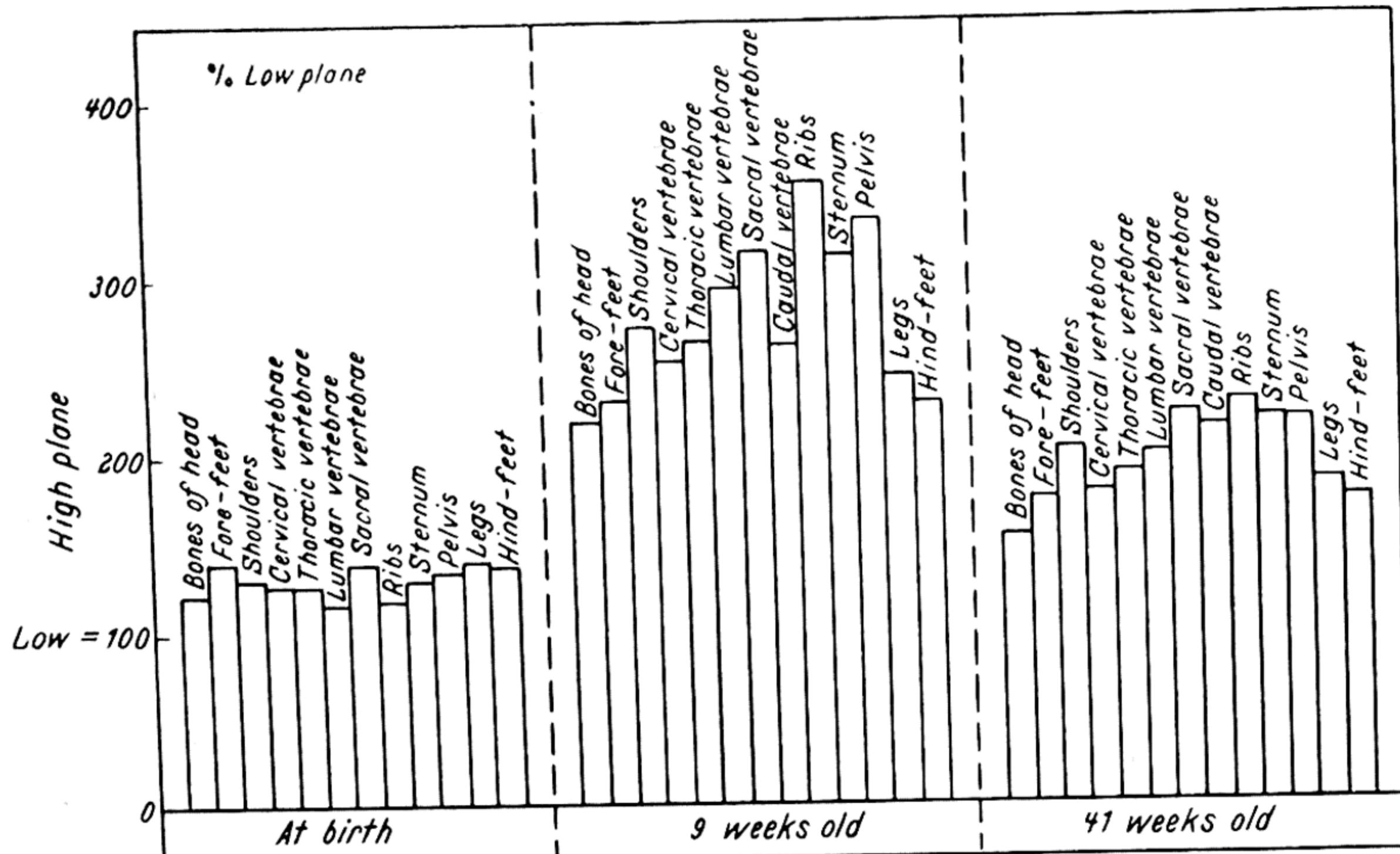


Figure 10.31. Effect of plane of nutrition on development of different skeletal parts in lambs with age. Compare with *Figure 10.13* and note the increasing retarding effects of the low plane feeding on the parts in an order of their increasing postnatal growth intensity. Weight of each part in High Plane lambs shown as percentage of the same part in the Low Plane ones at each age. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

thin and round. On the other hand the metacarpals of High plane lambs at 9 weeks and much more so at 41 weeks, have the thick flattened shaft characteristic of early maturing improved breeds (compare *Figures 10.33* and *10.34*). The effect of a Low plane of nutrition on the development of muscle, intermuscular fat and subcutaneous fat, as in the skeleton, exhibits a gradient from the early to the late maturing regions of the body in each case, the latest maturing parts being most and the earliest developing least affected (*Figures 10.35* and *10.36*).

Restricted nutritive supply during growth has great inhibiting effects on the normal development of sexual characteristics. As described on page 466, ewes are earlier maturing than wethers and during the earlier stages of postnatal growth exhibit relatively better development of the later maturing body regions and tissues than the wethers, while at mature weights the wethers attain a higher degree

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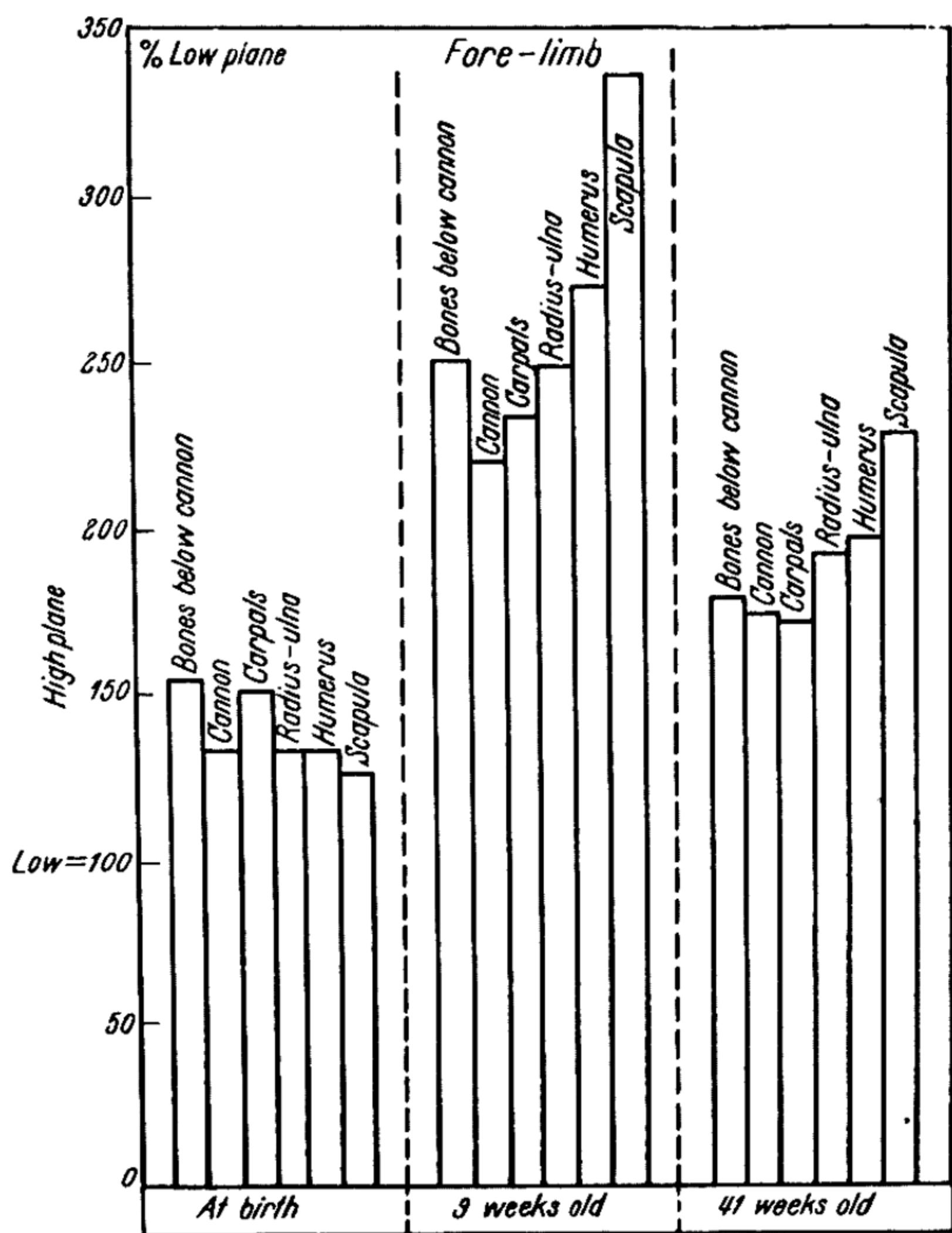
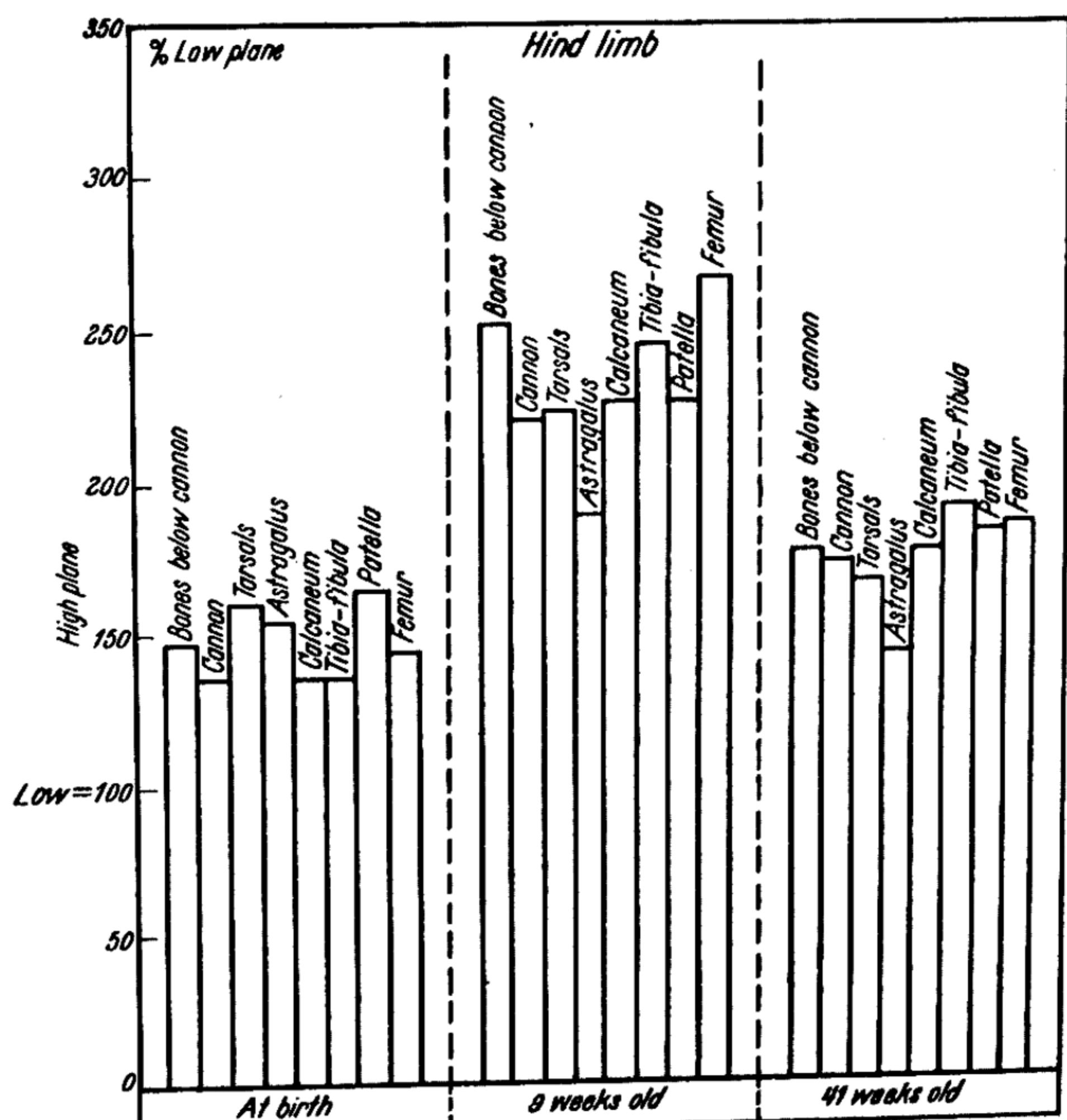


Figure 10.32. Effect of plane of nutrition on development of limb bones in lambs with age. Compare with *Figure 10.13* and note gradient of increasing retarding effects of the low plane feeding in the direct order of growth intensity of the bones at each age interval. Weight of each bone in High Plane lambs shown as percentage of the weight of the same bone in the Low Plane ones at each age. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)



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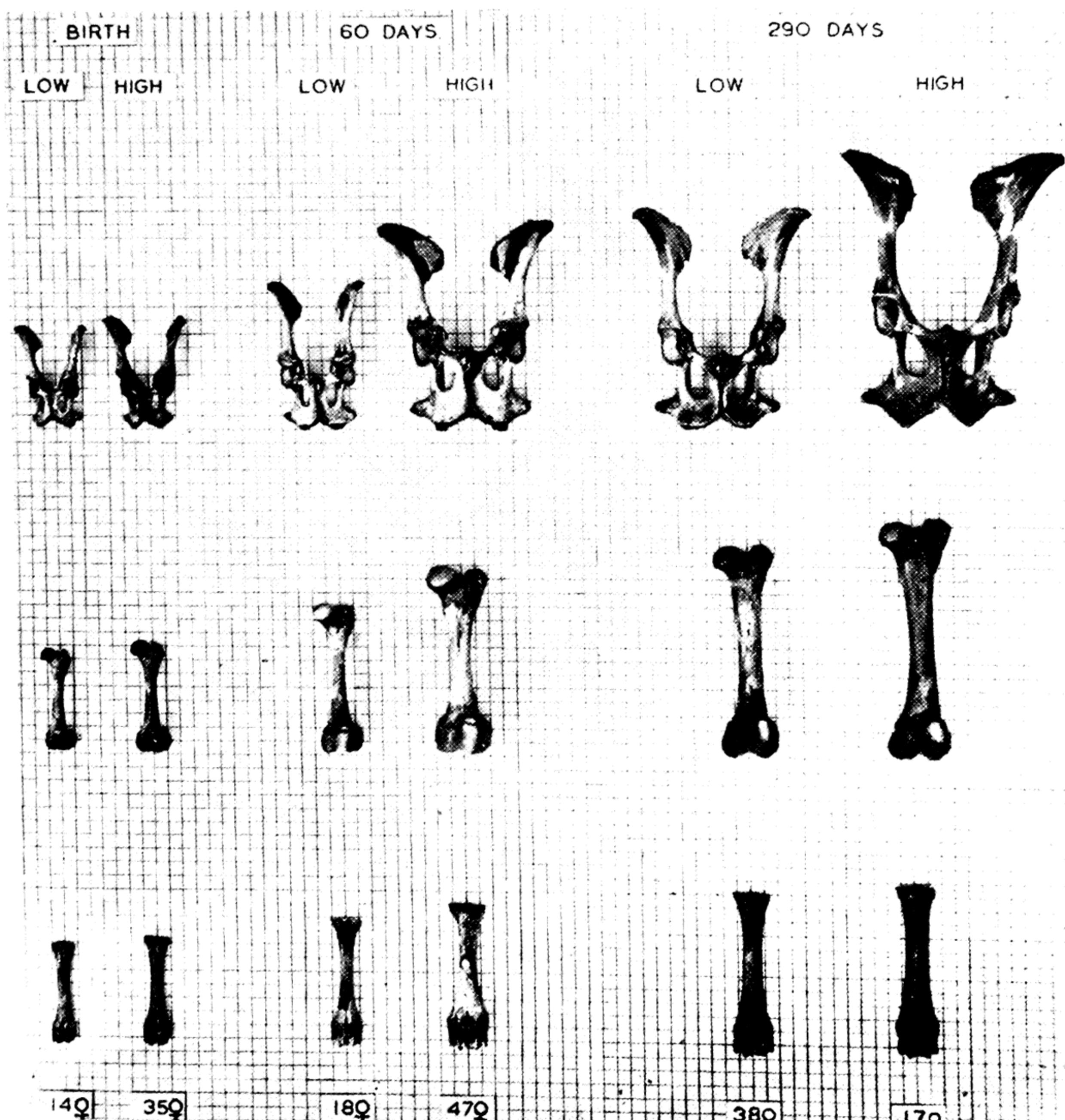


Figure 10.33. Effect of plane of nutrition on the size and shape of pelvis, femur and cannon in ewe lambs with age, showing greater retarding effects of the Low Plane feeding on thickness than length growth and proportionately greater retarding effects on the development of any bone at the age of its highest growth intensity: prenatally on the cannon and postnatally on the femur and pelvis. Compare with *Figure 10.34* and note the resemblance of the Low Plane cannons and those of unimproved breeds (Soay, Shetland and Merino). (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

of development than ewes, illustrated by their absolutely and proportionately better development of the later maturing tissues and body regions. Pálsson and Vergés (1952) found that a Low plane of nutrition up to 41 weeks completely suppresses the great advancement in the development of the later maturing characters in the wethers, so that at this age in the Low plane series the wethers are less advanced in the development of the later maturing characters than the ewes, exactly the reverse of what was found in the High plane series at the

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same age. The magnitude of the differences in relative body proportions is illustrated in *Figure 10.21*.

The extra growth in length and thickness of the long bones of the limbs in the wethers as compared with the ewes during the later stages of normal development is completely repressed by restricted nutrition. For example, in the Low plane group at 41 weeks, the fore cannons are slightly shorter and more slender in the wethers

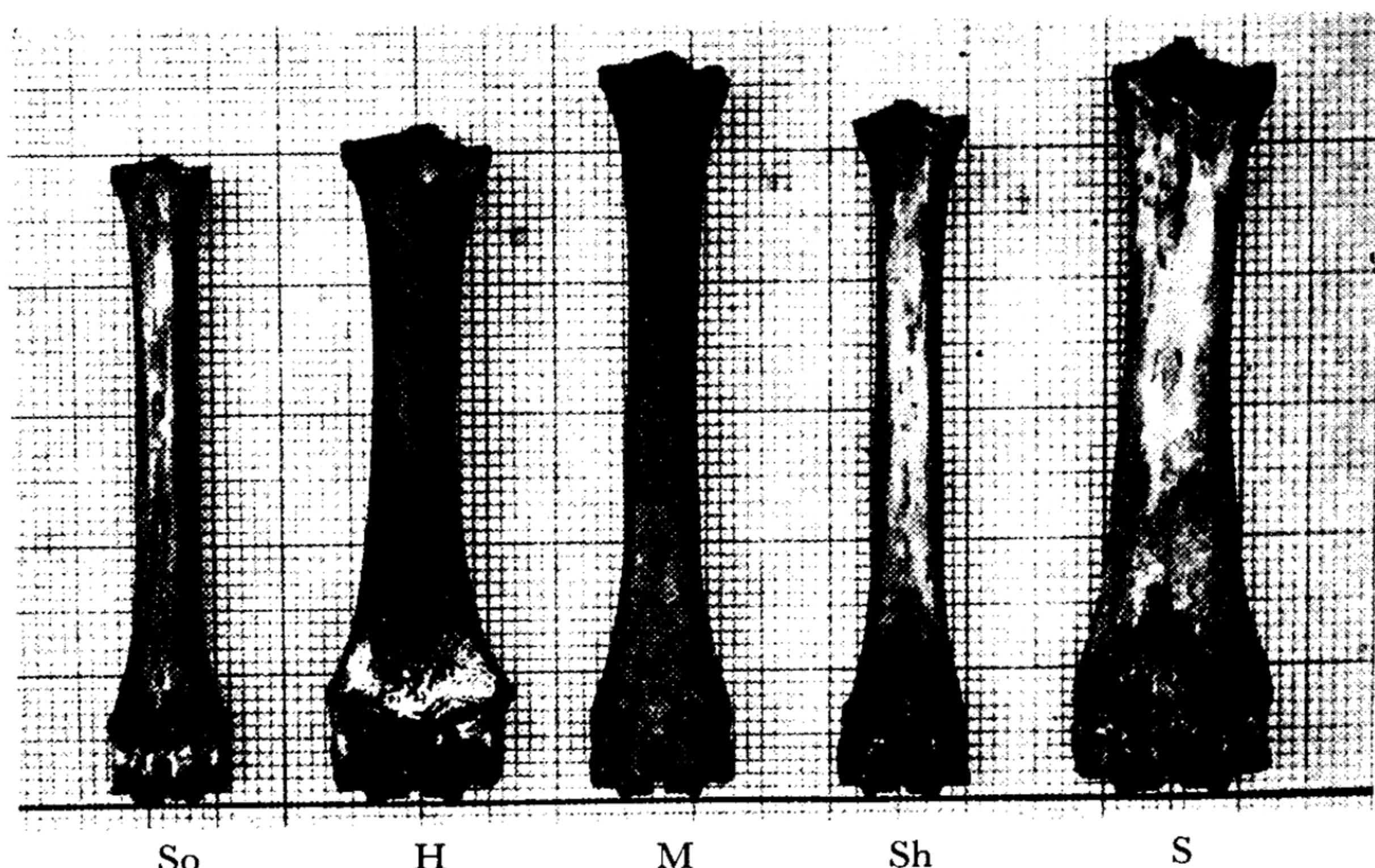


Figure 10.34. Effects of domestication on bone form in sheep—rams—showing greater development in thickness of the hind-cannon in the improved Suffolk (S) and Hampshire (H) breeds as compared with the unimproved Soay (So) and Shetland (Sh) and the wool breed Merino (M). (From Hammond, 1932a, by courtesy of Oliver and Boyd.)

than in the ewes, while in the High plane group this bone is considerably longer and much thicker in the wethers than in the ewes (*Figure 10.37*). The repressing effects of restricted nutrition on the normal development of the male characteristics in the long bones of the limbs increase in distal-proximal order (*Figure 10.23*), being much less pronounced in the early maturing cannon than in the later maturing femur; the latest maturing pelvis is by far the most affected, and still retains its narrow and slender juvenile form in the Low plane wethers at 41 weeks. In the Low plane ewes this bone, though also retarded in development does, however, attain a relatively much greater width (*Figure 10.23*).

A limited nutritive supply during growth has also depressing effects on the development of the primary sexual characters, *i.e.* the sex organs, especially during the later stages of development, when the growth intensity of these organs is at its highest level (*Figure 10.10*). At 9 weeks, for example, Pálsson and Vergés (1952) found that the

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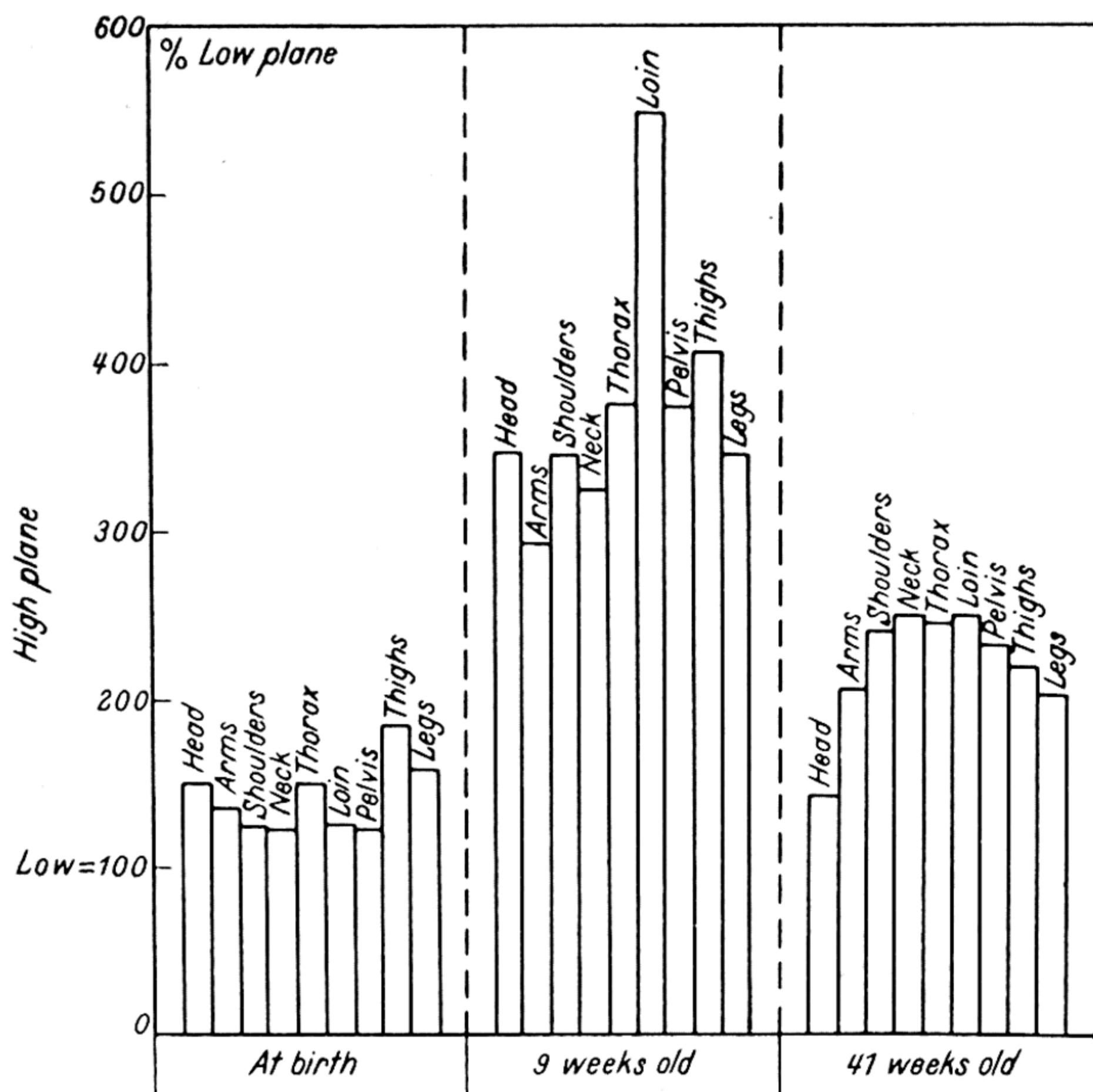


Figure 10.35. Effect of plane of nutrition on development of muscle in different joints in lambs with age, showing greater differential retarding effect of the low plane feeding in postnatal than prenatal life and proportionately greater effect on the late than the early maturing joints. Weight of muscle in each joint in High Plane shown as percentage of the weight of muscle in the same joint in the Low Plane at each age. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

uterus and vagina are least affected of all the abdominal organs, while at 41 weeks in the Low plane ewes they are relatively much more affected than most of the other organs (*Figure 10.26*).

As the different regions and tissues of the animal's body grow at different rates during the normal course of development it follows that an animal stunted by under-nutrition has different body proportions from one which at the same age has attained much greater weight. Stunting due to a Low plane feeding during certain periods of growth is not simply a postponement of development in general, *i.e.* the stunted animal is not merely anatomically younger than another which has been growing at a faster rate because of plentiful food supply, but the animal's form changes regardless of its size and weight (McMeekan, 1940, 1941, in the pig *see* pages 501-507; Pálsson and Vergés, 1952, in the sheep *see* pages 490-496). Pálsson and Vergés also compared animals (2) *at similar weights but different ages, and at the same age and weight but having differently shaped growth curves*. The treatment differences, the shape of the growth curves and the age at

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slaughter of the four groups of lambs compared at the same dressed carcass weight of 30 lb. by Pálsson and Vergés (1952) are described on page 478 and illustrated in *Figure 10.25*. Their results show that the different treatments affect the body conformation and the development of the different organs and tissues differentially. The carcass percentage is highest in the High-High group, 48.9; lowest in the

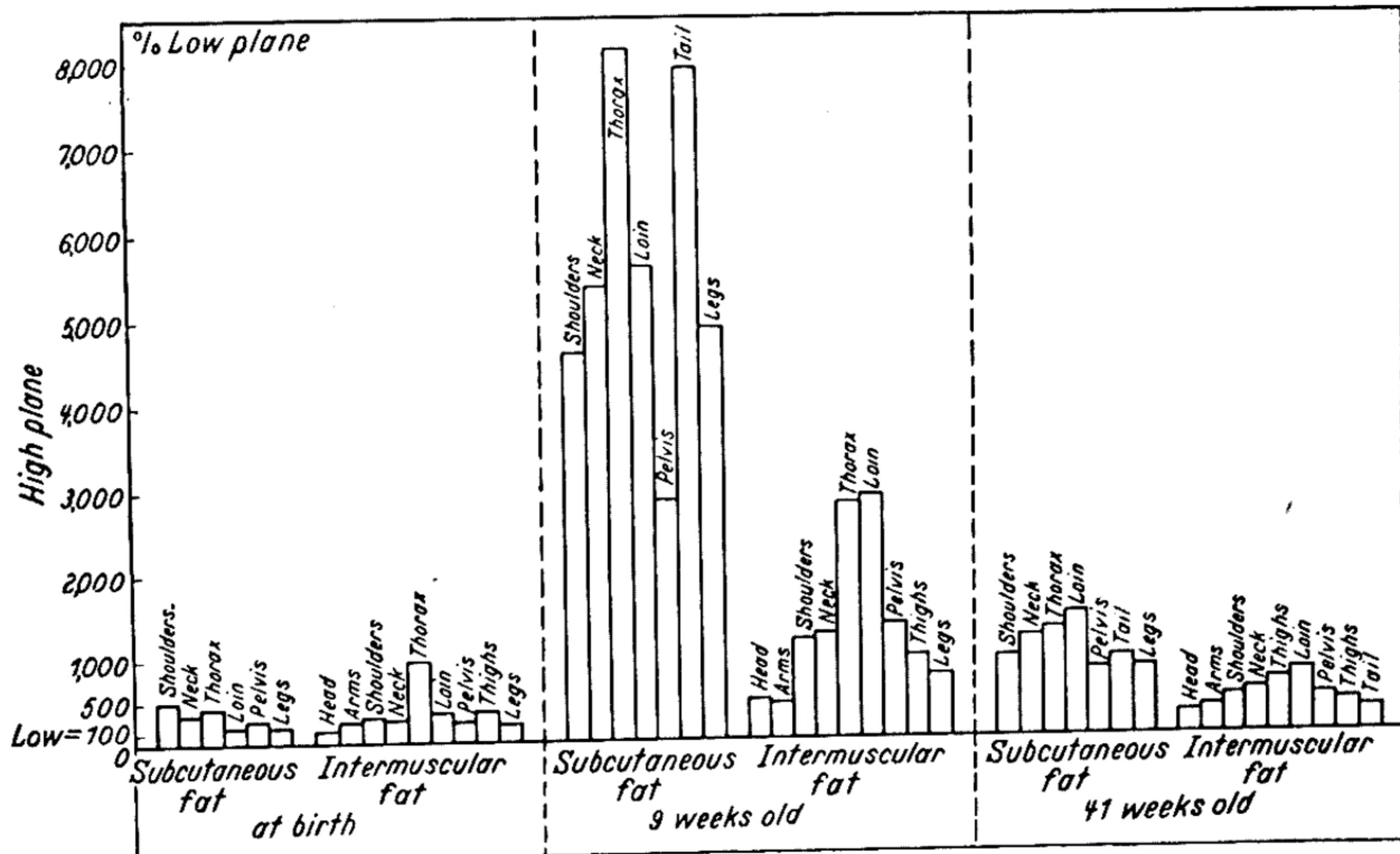


Figure 10.36. Effect of plane of nutrition on relative development of subcutaneous and intermuscular fat in different joints in lambs with age. Note greater retarding effects of the low plane feeding on the development of subcutaneous fat in postnatal life and on both subcutaneous fat and intermuscular fat in the late than in the early maturing joints. Weight of fat in each joint in High Plane lambs shown as percentage of the weight of fat in the same joint in the Low Plane ones at each age. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

Low-Low group, 42.9; and intermediate in the High-Low and Low-High groups. The weight of the head is more affected by the age of the animal than by the plane of nutrition or the carcass weight, it being of the same weight in the High-Low and Low-High groups, lightest in the youngest, High-High group, and heaviest in the oldest, Low-Low group. Similarly the brain and the eyes appear to be primarily a function of age, indicating their high priority for available nutrients. The development of some of the internal organs is greatly affected by the plane of nutrition, while others are rather a function of age; some, such as the heart, appear to be a function of the weight of the carcass, it being of similar weight in all treatment groups. The development of the thymus glands, the liver, the spleen, the kidneys, and the small intestine as well as the blood is more dependent

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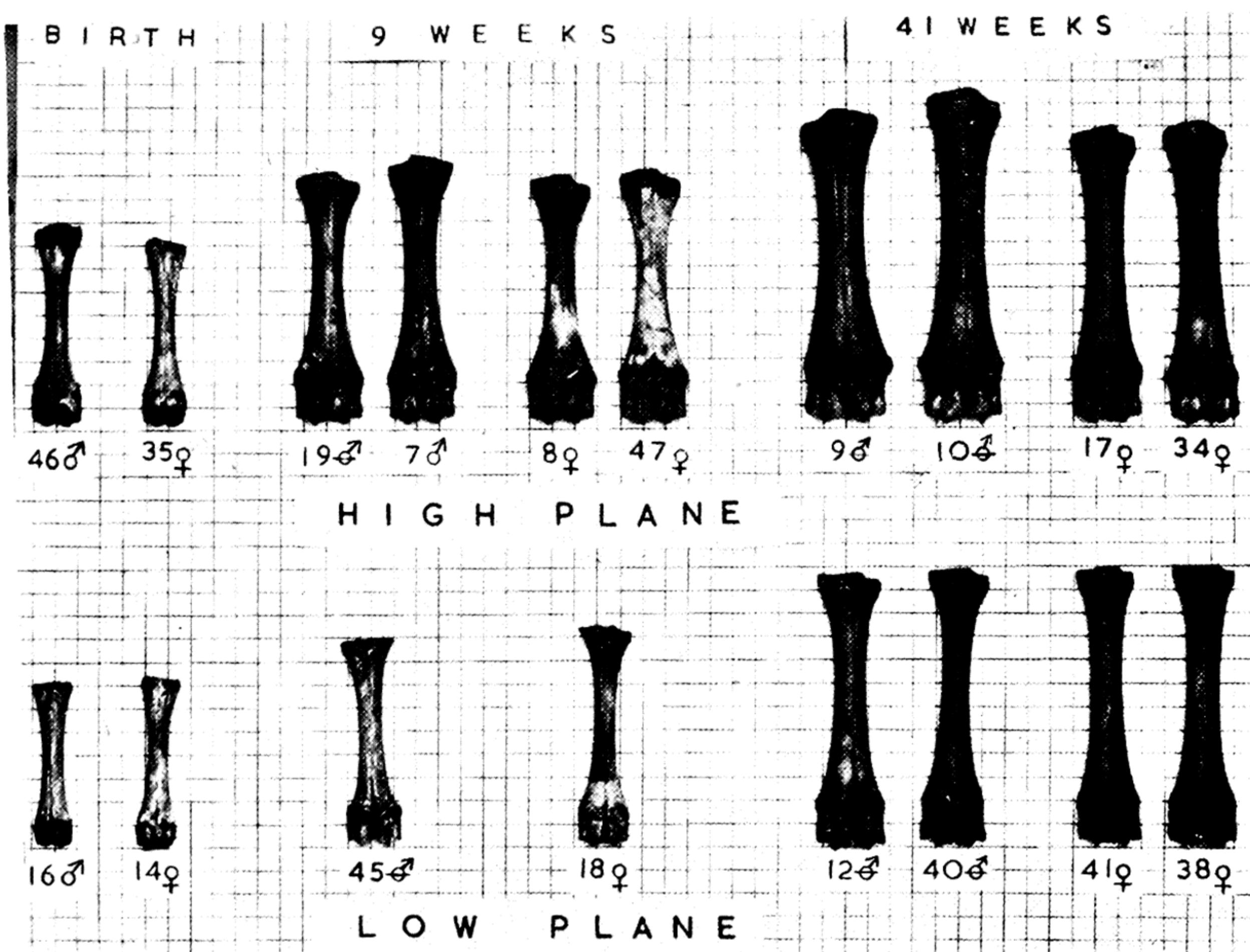


Figure 10.37. Effect of plane of nutrition on development of sexual differences in the size and shape of bones in lambs with age, showing how a low plane feeding completely checks the extra development in length and thickness of the forecannon in the wethers. Compare with Figure 10.34 and note that the cannons of the Low Plane lambs at 41 weeks resemble more the cannons of the unimproved breeds (Soay, Shetland and Merino) than those of the same breed and age reared on a high plane nutrition. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

on the level of nutrition just prior to slaughter than on age or carcass weight; these organs are significantly heavier in the High-High and the Low-High groups than in the High-Low and the Low-Low ones. On the other hand the development of organs like the oesophagus, the rumen, the reticulum and the omasum appears to be more influenced by age than by the plane of nutrition, while that of the abomasum, the large intestine and the pancreas is influenced by the plane of nutrition as well as by age. The organs in general appear to have a priority claim for the available nutrients in the blood stream to allow them to develop to such an extent to enable them to cope with their function at any age; this is reflected in the lower dressing percentage of animals reared on a low plane of nutrition. Under limited nutritive supply, organs whose function is directly associated with growth suffer proportionately more than those, like the brain, the eyes, and the heart, which are of primary importance for life.

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The four treatments produced two distinct types of carcasses (*Figure 10.38*). The High-High and Low-High carcasses are of very similar conformation. They are short in the leg, blocky and well covered with subcutaneous fat, with the later maturing trunk joints proportionately better developed than in the High-Low and Low-Low

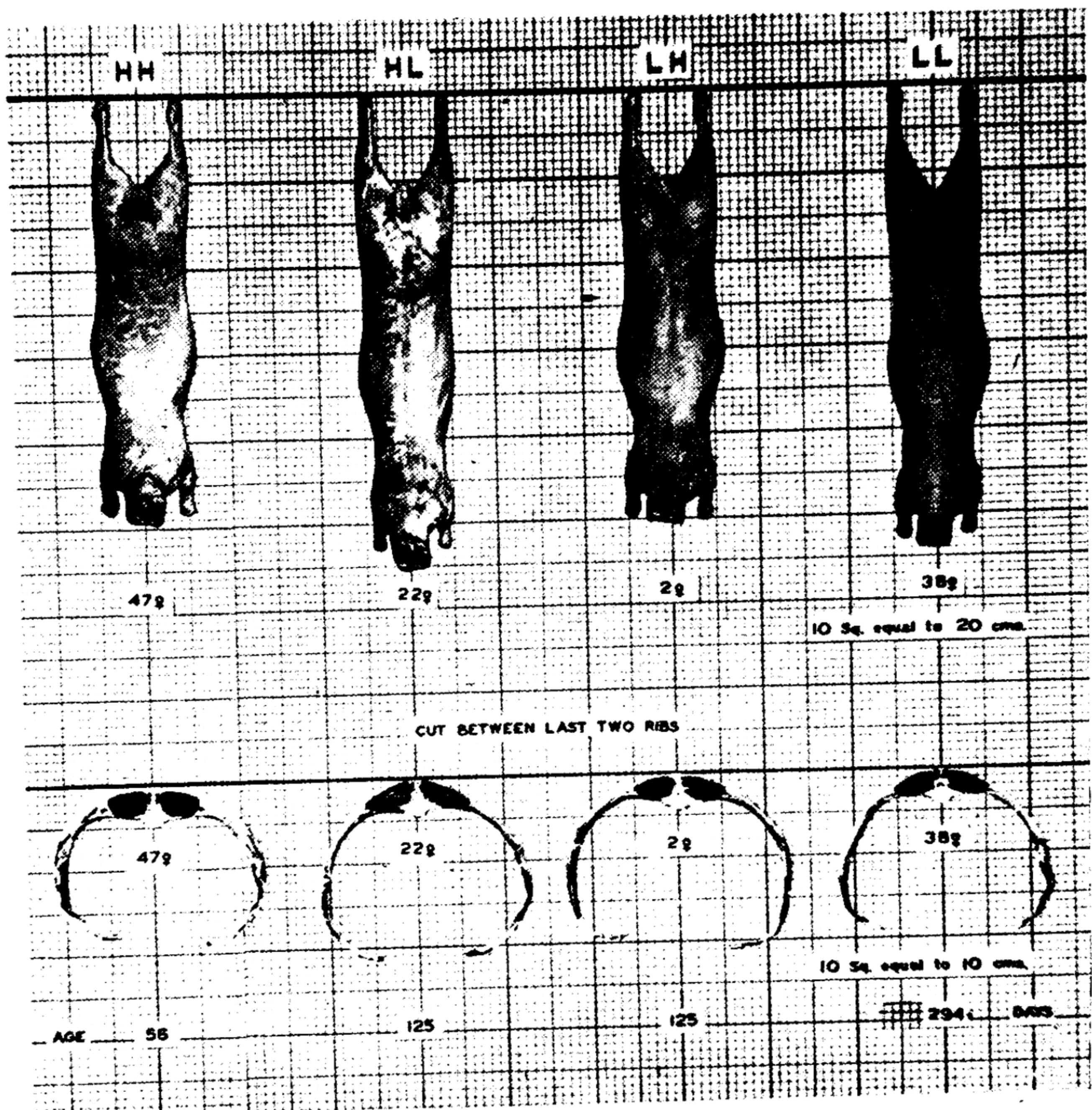


Figure 10.38. The effect of the shape of the growth curve (see *Figure 10.25*) on the carcass conformation of lambs at the same carcass weight (30 lb.). (From Vergés, 1939a, by courtesy of *Suffolk Sheep Society Year Book*.)

carcasses, which in general conformation resemble each other, being leggy, lank and poorly covered with subcutaneous fat. In the latter two groups the early maturing legs and neck are better developed than the later maturing trunk joints (*Figure 10.39*). *Figure 10.40* shows the differential effects produced by the four treatments on the

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carcass composition. Bone weight in the dressed carcass is significantly lighter in the Low-Low than in the other groups in spite of the greater length of the individual bones. This is due to the inhibiting effects of continuous under-nutrition on bone growth in thickness. Bone is heaviest in the High-Low group because of its rapid gain in weight

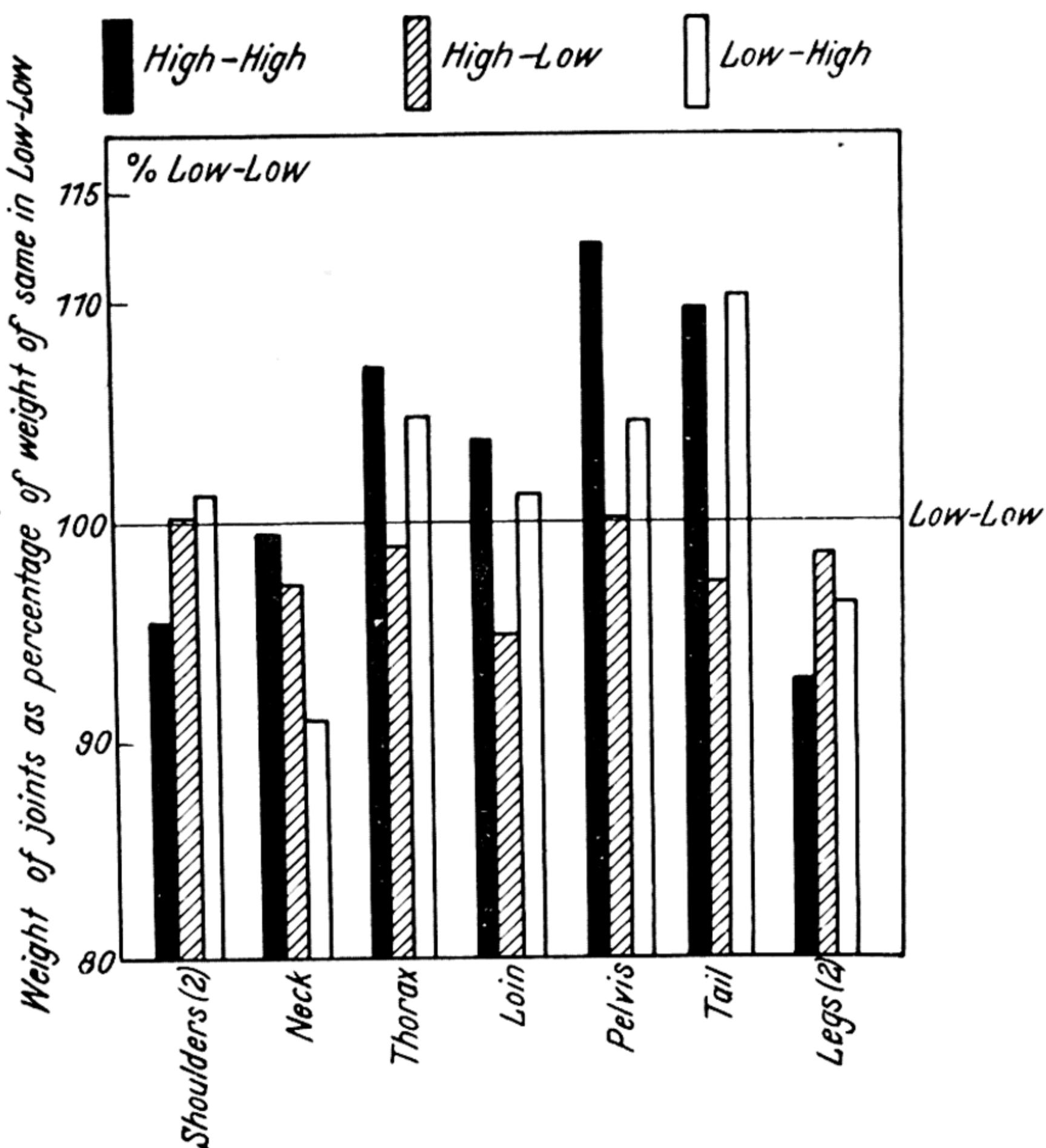


Figure 10.39. The effect of the shape of the growth curve on the proportions of different joints in lambs at 30 lb. carcass weight. (Weight of each joint in Low-Low = 100.) (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

at an early age when the nutritive supply was plentiful; at this time growth intensity of bone is very high, and after the nutritive supply is reduced bone continues to gain at a fairly rapid rate due to its high priority for the available nutrients. Muscle is better developed in the High-Low and Low-Low groups than in the Low-High and High-High ones, while fat, especially subcutaneous fat, is better developed in the latter groups. A High plane of nutrition prior to slaughter appears to be essential for good development of the latest maturing tissues, such as the subcutaneous fat, for under limited food supply the earlier maturing tissues, muscle and bone, especially for growth in length, have priority claims for the available nutrients (see page 476). This is of great practical importance for the producer of fat lamb as a

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certain minimum development of subcutaneous fat is essential for first quality lamb carcasses (see page 581).

As between the different tissues, so between one tissue in different anatomical units of the body marked differential effects were produced by the four different treatments. In general, limited nutritive supply at any age has the greatest inhibiting effect on the tissues, or those parts of any one tissue, which at that age have the highest growth intensity. Good nutrition at any age also benefits most the parts of highest growth intensity at that age. All the tissues show great

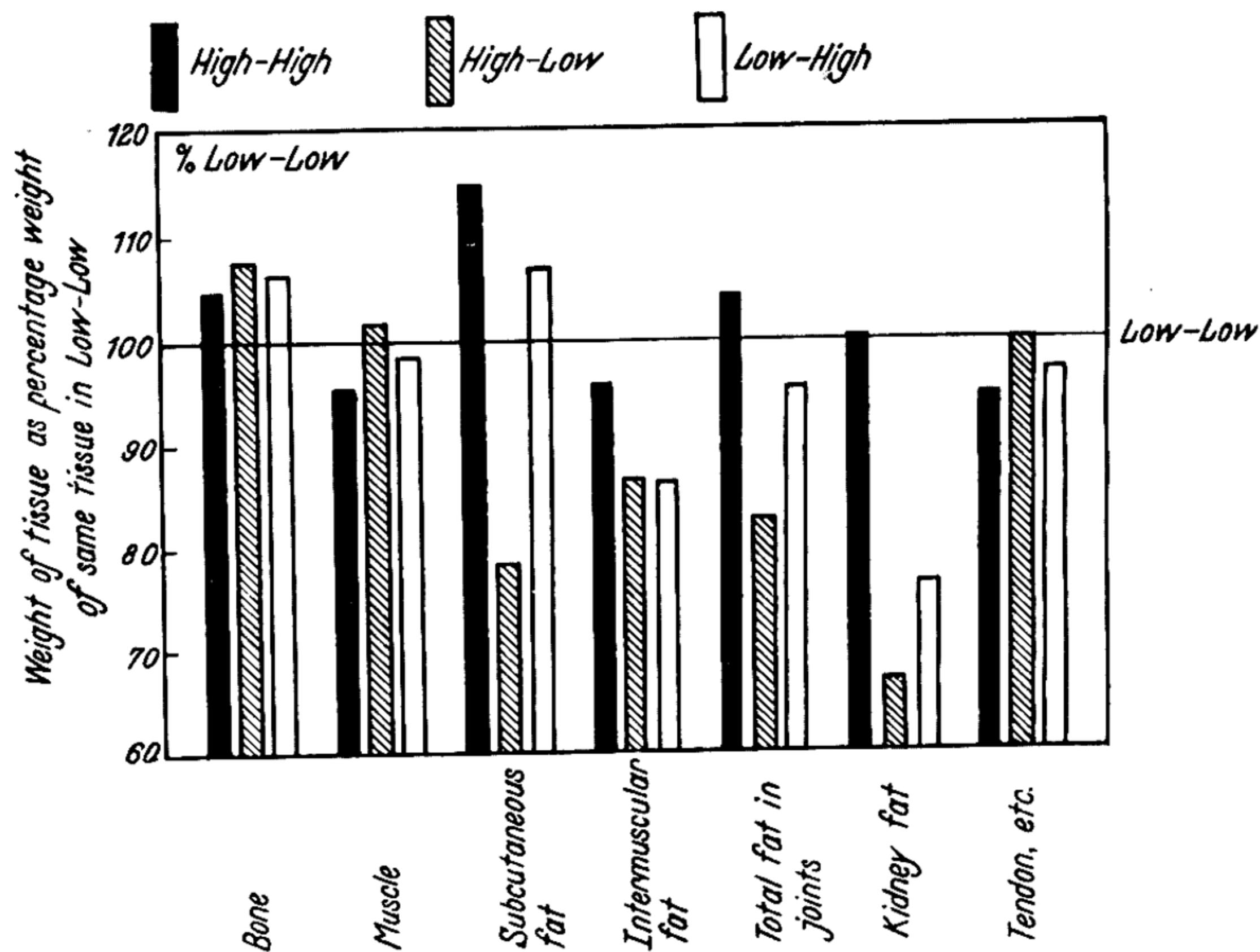


Figure 10.40. The effect of the shape of the growth curve on composition of dressed lamb carcasses at 30 lb. (Weight of each tissue in the Low-Low lambs taken as 100.) (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

recuperative capacity if provided with adequate nutritive supply after restricted nutrition, unless the particular tissue has passed the age of active growth. For example, comparison of the High-Low and Low-High lambs, which were killed at the same age and weight, shows that the restricted nutrition from 6-15 weeks which followed high feeding from the 90th day of foetal life to six weeks in the former, resulted in much greater retardation in development of the subcutaneous fat, the tissue of highest growth intensity at that age, than of any other tissue; furthermore, all tissues in this group were relatively more affected in the later maturing than in the earlier maturing regions of the body. The High plane feeding from 6-15 weeks, following severe under-nutrition from the 90th day of foetal

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life to six weeks in the Low-High lambs, on the contrary, resulted in proportionately better development of the subcutaneous fat than the other tissues, and within any one tissue a proportionately better development in the later maturing than in the earlier maturing parts of the body. Comparison of the different anatomical units of the major tissues of the High-High and the Low-Low carcasses showed that within each tissue the latest maturing parts suffered proportionately more from the continuous under-nutrition of the Low-Low lambs. The exception to this is found in the ribs, which, although they are the latest maturing part of the skeleton, were as heavy in the Low-Low as in the High-High lambs, though all other skeletal parts of the former were lighter than in the latter. This is considered to be due to the very late onset of high growth intensity in the ribs. The High-High lambs were killed before the ribs could benefit as much as the earlier maturing parts of the skeleton from the good nutrition. On the other hand, in the Low-Low lambs, the ribs, having a high growth intensity for a long time after the growth rate of the earlier developing parts of the skeleton had declined, could compete for nutrients with still later maturing tissues such as muscle and fat with considerable success.

The shape of individual bones is much more affected by the different planes of nutrition than is their weight. The earlier maturing growth in length is, however, less affected than the later maturing growth in thickness. The earlier maturing distal bones of the limbs, such as the cannon, are also less affected than the later maturing proximal bones such as the femur and the pelvis (*Figure 10.41*). The four different treatments affect the shape of the fore cannons differentially (*Figure 10.42*). There is but slight difference in shape of this bone in the High-High and Low-High groups, both being relatively short with thick shafts, typical of improved breeds. The cannons of the Low-Low group are long and slender, resembling those of unimproved breeds (see page 488, *Figure 10.34*), while those of the High-Low are in an intermediate position. The significantly shorter cannons in the Low-High as compared with the High-Low group illustrates the inhibiting effect of Low plane nutrition on length growth in the former during the high growth intensity period of the late foetal and first few weeks of postnatal life. This is probably of a permanent nature for it is not made up during 9 weeks of plentiful food supply, from 6-15 weeks, because by then the intensity of growth in length of this early maturing bone has already greatly declined; its growth in thickness, however, is still active, thus enabling it to make up for previous retardation in thickness growth. The greater inhibiting effects, caused by limited food supply on growth in weight and thickness as compared with growth in length of the fore cannon is illustrated in *Figure 10.43*. In all thickness measurements and weight the High-High cannons are relatively best developed while the Low-

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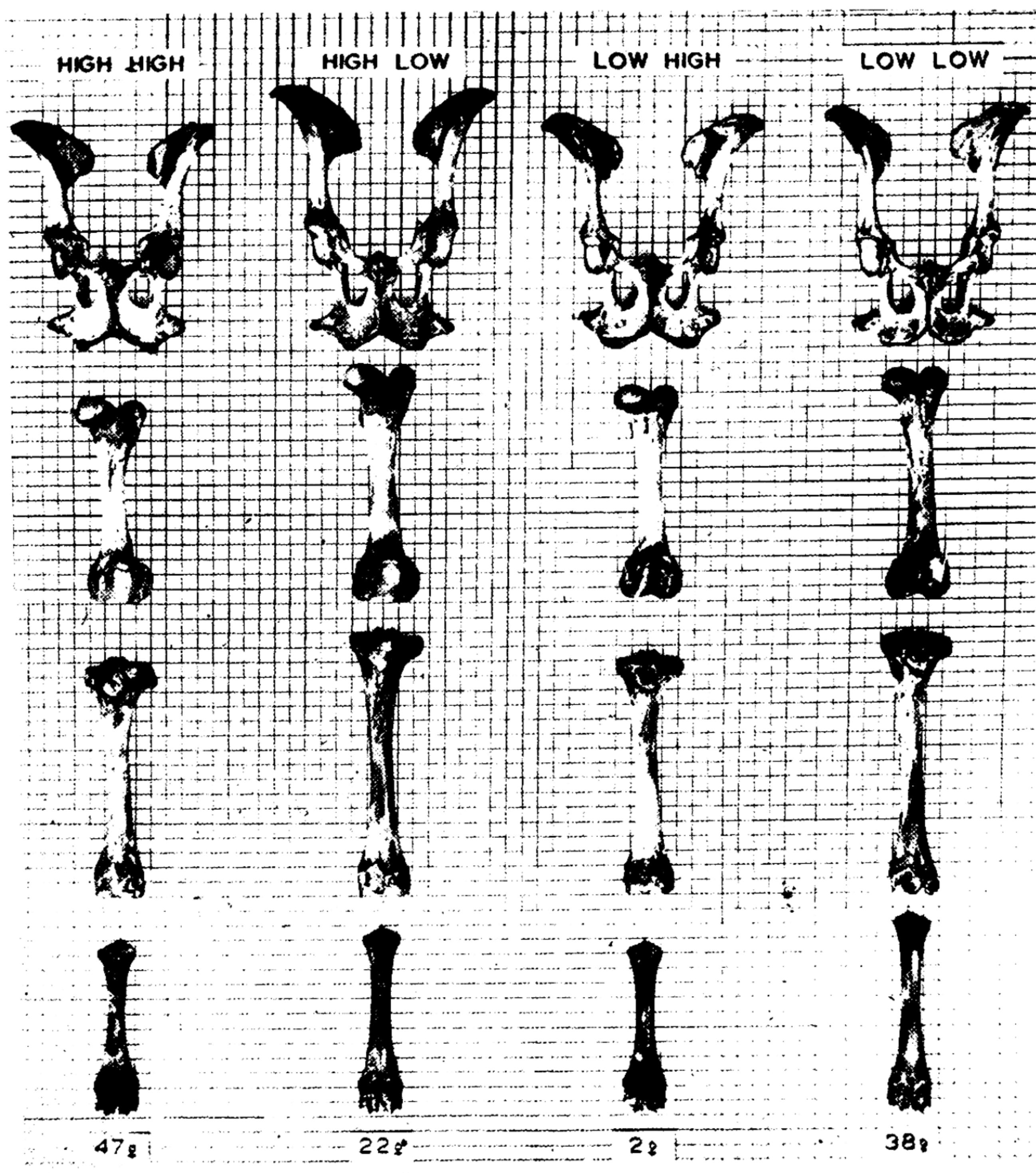


Figure 10.41. The effect of the shape of the growth curve on the size and shape of bones of the hind limb in lambs of 30 lb. carcass weight but at different ages, showing the resemblance in bone form between the High-High and Low-High lambs and between the High-Low and Low-Low lambs. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

Low ones are longer, lighter and less well developed in all measurements indicative of thickness than the cannons in any of the other groups.

Cattle

As in sheep, the normal age-changes in body proportions can be altered by controlling the growth curve of the animal. Although the effect of different planes of nutrition on the development of body

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proportions in cattle have not been studied in as great detail as in sheep and pigs, nevertheless ample evidence is available showing that restricted nutrition while the animal is still growing affects the various body regions differentially in general along the same lines as has been described above in sheep. In his pioneer work Waters (1908, 1909), keeping young steers on maintenance and sub-maintenance rations for certain length of time, found that the steers continued to grow in some directions and change in conformation at the same time as they were losing, or barely maintaining, their body weight. The steers

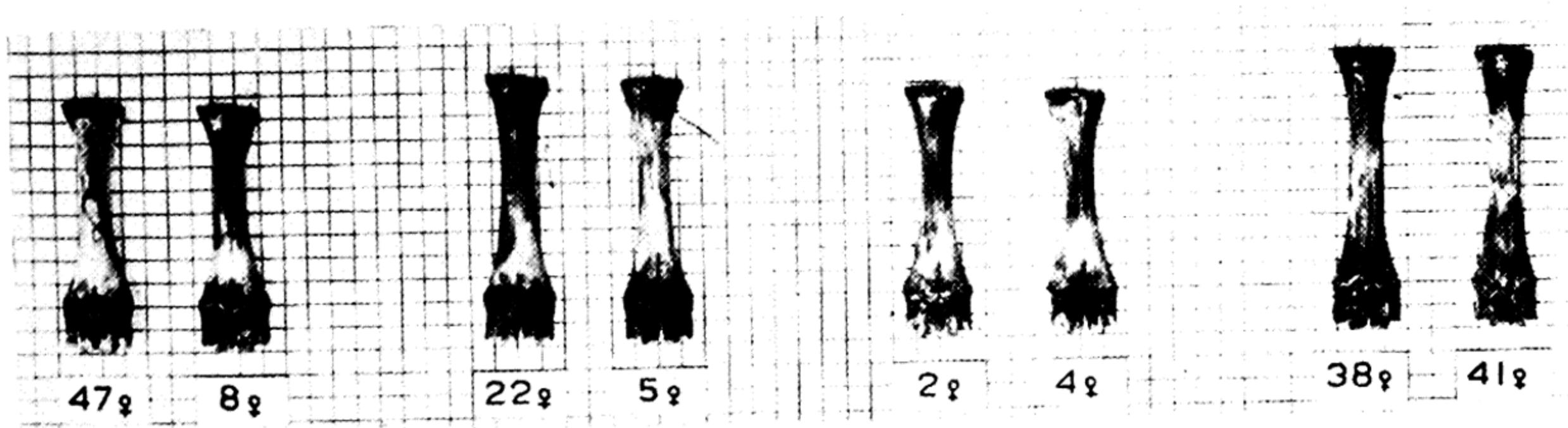


Figure 10.42. The effect of the shape of the growth curve on the form of the fore-cannon in lambs of 30 lb. carcass weight, showing short relatively thick cannons in the High-High and Low-High lambs as compared with long thick cannons in the High-Low and long thin cannons in the Low-Low ones. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

increased in height at withers and in length of head due to length growth of the bones, while the width measurements at hips and chest decreased, so the animals became relatively large but narrow and thin. By inspection of the carcasses and chemical analysis to supplement the body measurement data, Waters was the first to establish scientifically the fact that bone in a young animal on sub-maintenance ration continues to grow, at least in length, even at the expense of previously stored up fat reserves in the body, thus demonstrating the priority claim, which the early maturing bone has for the available nutrients in the blood stream. Waters (1909), and later his collaborators and followers (TROWBRIDGE, MOULTON and HAIG, 1918-23) at the Missouri Agricultural Experimental Station, studied also the effects of different levels of nutrition on the weight of different parts of the body (using butchers' joints) and found that the later maturing regions, such as the loin and pelvis, are more severely penalized by under-nutrition than the earlier maturing neck, brisket and the fore-quarters in general. Numerous workers have since shown that restricted nutrition, either seasonally or continuously during the growing period, affects the various body measurements differentially in a direct order of their maturity (see page 498), *i.e.* those which develop rapidly in early life, such as the head measurements and the height at withers, are least affected, while those which develop late,

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such as the width measurements in the pelvic regions, are most affected (see Prawochenski and Kaczkowski, 1926; LUSH *et al*, 1930; SCHUTTE, 1935; GUILBERT *et al*, 1944; STEENSBORG, 1940; STEENSBORG and ØSTERGAARD, 1945; BONNIER, HANSSON and SKJERVOLD, 1948;

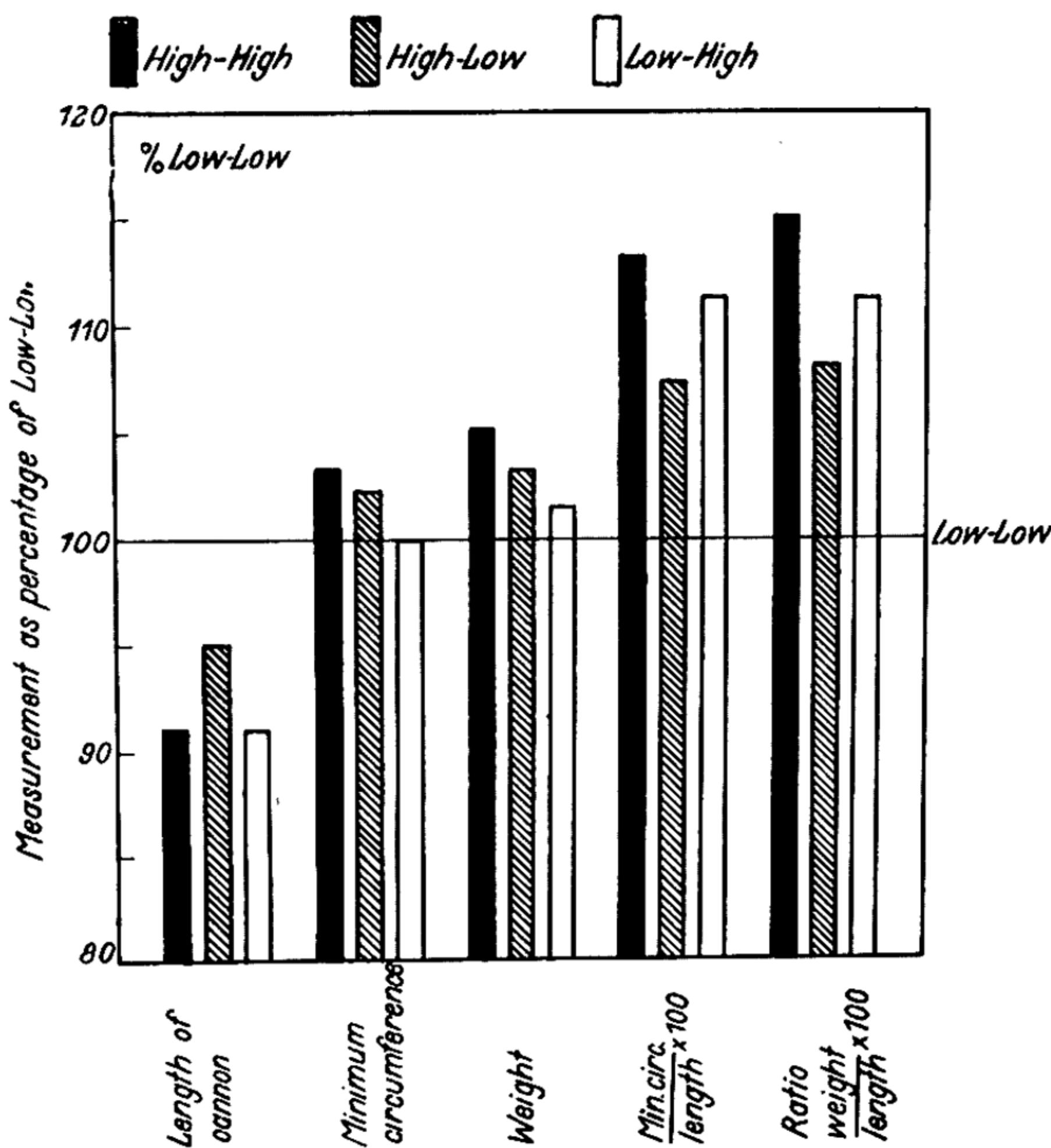


Figure 10.43. The effect of the shape of the growth curve on measurements and weight of the left fore-cannon in lambs of 30 lb. carcass weight, showing the longest, lightest and most slender cannons in the oldest Low-Low lambs and the shortest, heaviest and thickest cannons in the youngest High-High lambs. (From Pálsson and Vergés, 1952, by courtesy of *J. agric. Sci.*)

HANSSON and BONNIER, 1950; Hansson *et al*, 1953; JOUBERT, 1954). In general, cattle reared on a Low plane of nutrition retain the juvenile form; they are leggy, narrow and shallow in the body, especially in the hind-quarters, with long, large heads, as compared with animals of the same breed, even identical twins (Figure 10.44), which are reared on a High plane of nutrition. As in sheep, limited nutritive supply largely inhibits the normal development of secondary sexual characters in cattle (Figure 10.45; FREDERIKSEN, 1929). At 25½ months the poorly fed Red Danish bull (Figure 10.45) not only resembles an individual of an unimproved breed, but also lacks completely the masculine characteristics, exemplified by the thick-crested neck and

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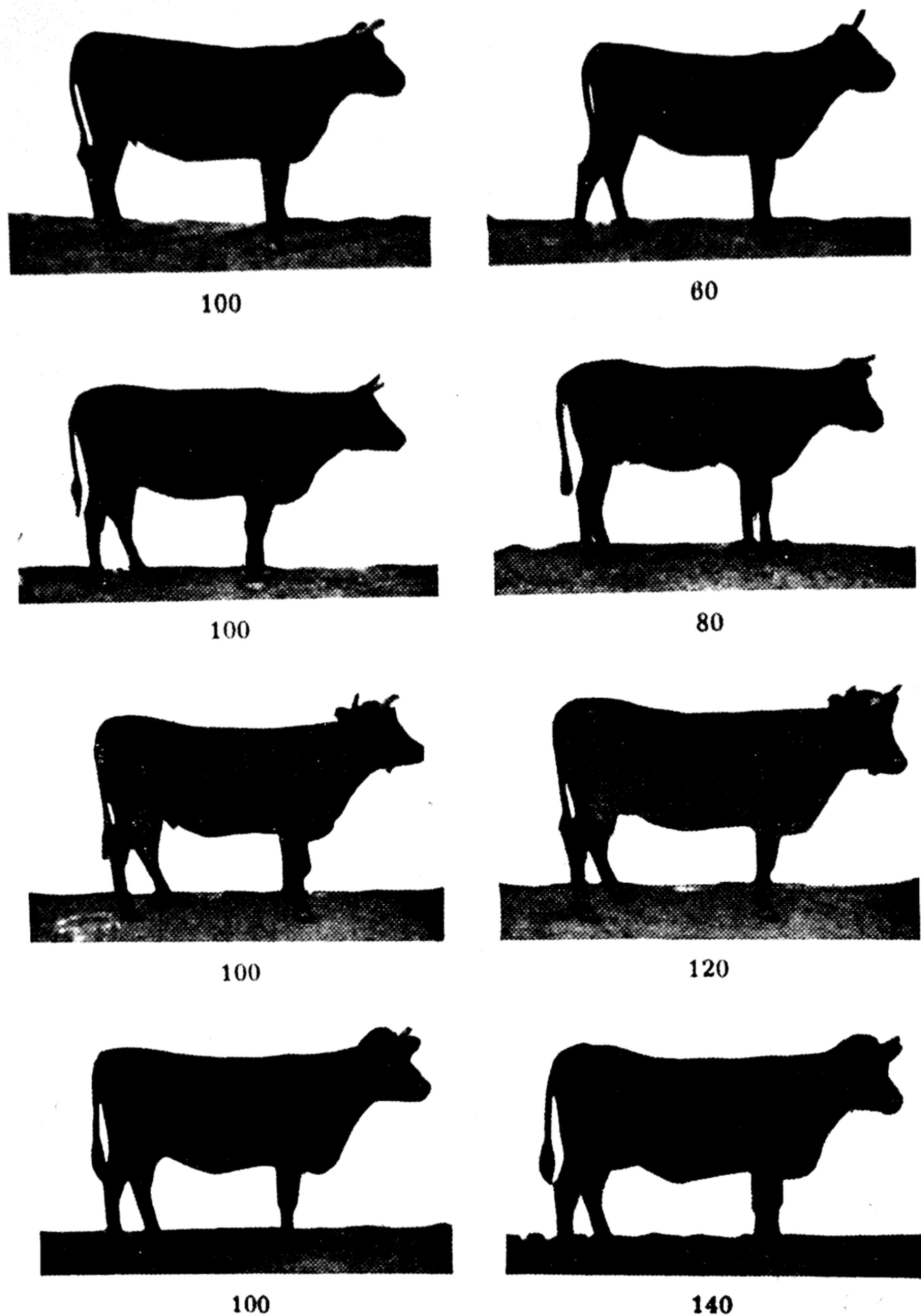


Figure 10.44. Effect of plane of nutrition during rearing on conformation of identical twin heifers at 22-24 months of age. Standard fed control twins on the *left*. Experimental twins on the *right*. The figures under each animal indicate the relative level of nutrition from month after birth. Note the large head, long legs and shallow body of Low plane heifer (*top right*) as compared with the deep blocky High plane one (*bottom right*). (From Hansson *et al*, 1953, by courtesy of *Acta agric. Scand.*)

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deep, well-developed fore-quarters in general, of the well-fed bull of the same breed and age. All external body measurements, which have been retarded in development by low plane feeding show great recuperative power, both in beef and dairy cattle, if the animals are changed on to a higher level of nutrition before the age of growth ceases. Furthermore, growth continues for a longer time in an underfed than in a well fed animal (Bonnier *et al*, 1948), so that in many cases animals which are underfed periodically, or not too severely for a longer period, are capable of full recovery. However, if under-nutrition is too severe or goes on for too long a period the

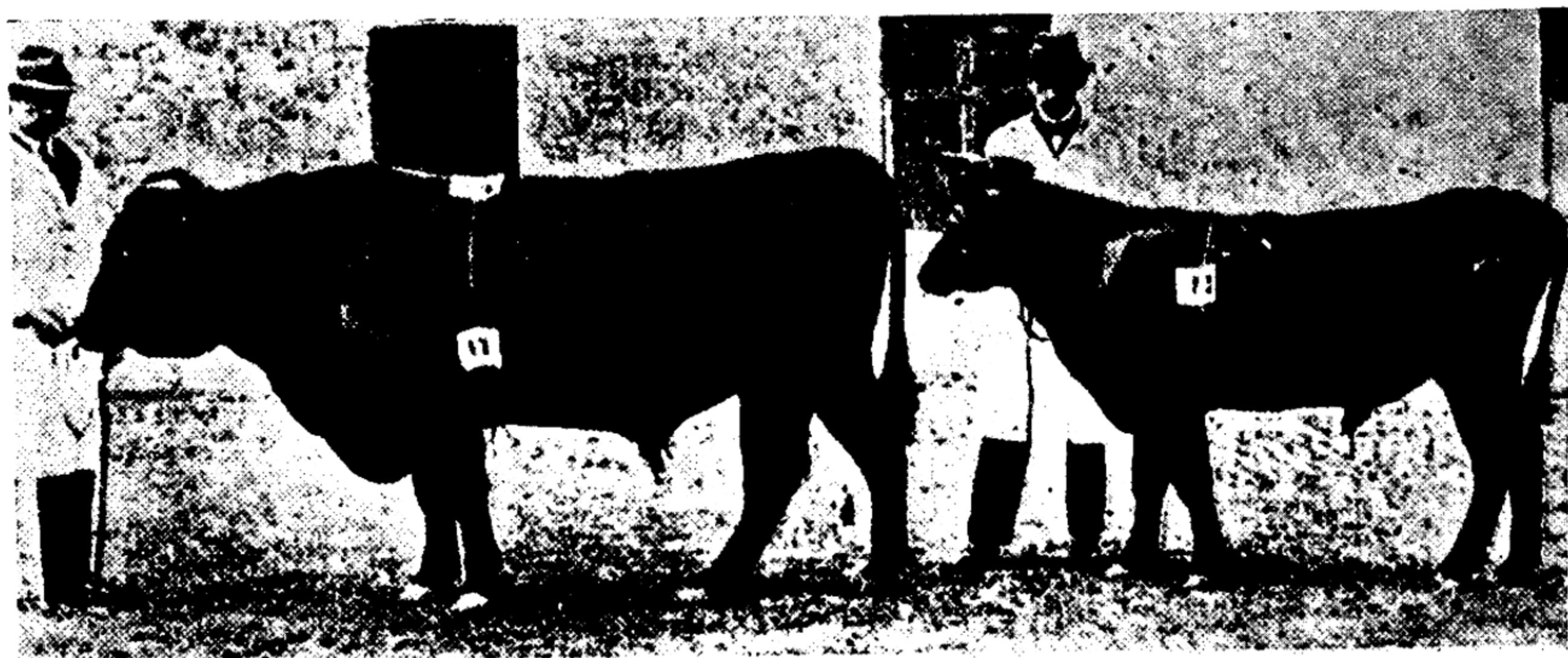


Figure 10.45. Effect of the plane of nutrition during rearing on size, conformation and male characters of Red Danish bulls by same sire. *Left*—Well reared: 3,998 food units fed; 2 years 45 days; 1,558 lb. liveweight. *Right*—Badly reared: 1,387 food units fed; 2 years 44 days old; 702 lb. liveweight. (From Frederiksen, 1929, by courtesy of *Ber. fra H.J.F. Kongres.*)

animals are permanently stunted so that their conformation as adults differs from their genetically determined phenotype (Eckles and Swett, 1918; Hansson and Bonnier, 1950; Joubert, 1954). However, breeds differ greatly in their recuperative capacity after stunting by restricted nutrition. In early maturing breeds growth ceases at a much younger age than in late maturing breeds. Steensberg and Østergaard (1945), for example, found that, even after the third calving, Shorthorn cows remained permanently stunted by a degree of under-nutrition during growth, which had no permanent stunting effects on either Red Danish or Black and White Jutland cattle. Joubert (1954), in South Africa, comparing the effects of High and Low levels of nutrition during growth on body development in two beef breeds—the Shorthorn and the Afrikaner—and two dairy breeds—the Friesian and the Jersey—also found that at $4\frac{1}{2}$ years much greater permanent stunting effects were observed in the early maturing Shorthorn than in the late maturing Afrikaner, and somewhat greater in the large Friesian than in the small Jersey breed.

Horses

Although direct experimental evidence on the effects of restricted nutrition on the development of body proportions in horses is seriously lacking, this species will undoubtedly follow the same general trend in this respect as other farm animals, *i.e.* that the later maturing characteristics, as the width measurements of the body, will suffer relatively more under adverse conditions than the early maturing characters like the height measurements. An exception to this probably occurs in prenatal life, when the length growth of the limb bones may be relatively more affected by severe under-nutrition of the dam than some other parts of the body, owing to the very high growth intensity in length of the limb bones at that stage (*see* page 449).

Pigs

As stated above (page 475) the normal age changes in body proportions as well as the relative development of different tissues and organs of the body in pigs can be altered at will by controlling the quantity of food intake in different stages of growth and thus change the shape of the growth curve (McMeekan, 1938, 1940; McMEEKAN and HAMMOND, 1939). In an inbred strain of Large

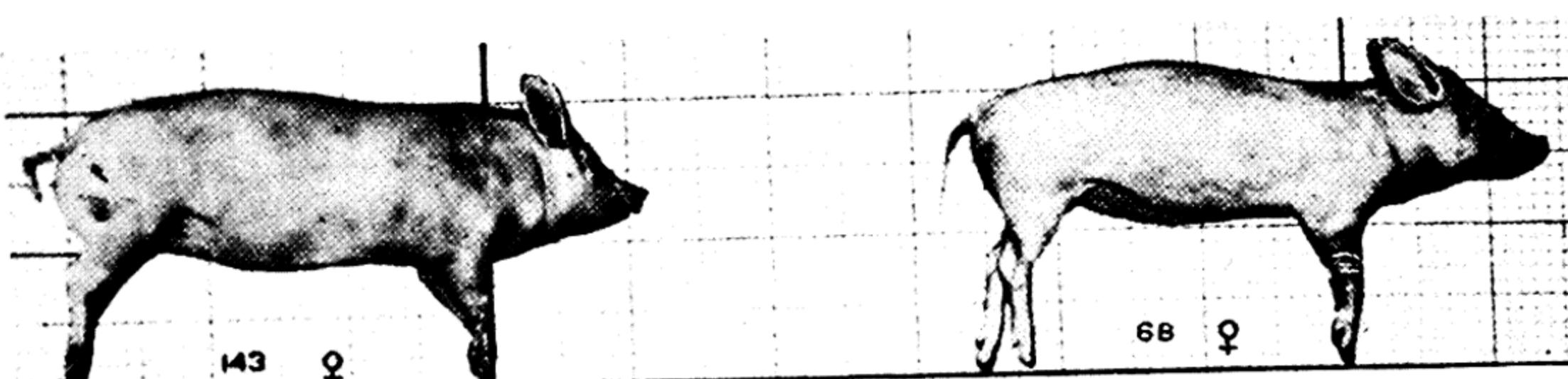


Figure 10.46. Effect of plane of nutrition on body conformation in pigs at 16 weeks. *Left*—High plane from birth, results in long body and well developed loin and hams. *Right*—Low plane from birth, results in large head, long legs and short shallow body with poor loin and hams. (From McMeekan, 1940, by courtesy of *J. agric. Sci.*)

White pigs, McMeekan (1940) compared (A) *the proportional development of different parts, tissues and organs of the body at 16 weeks in two groups which had been reared on two widely different—High and Low—planes of nutrition from birth.* At this age the live weight of the High plane was 113 lb. as compared with 37 lb. for the Low plane pigs. Furthermore, he compared (B) *the relative development of the different body regions and tissues in four groups of pigs, of the same strain, at 200 lb. live weight.* These had been made to follow four different predetermined growth curves so as to reach 200 lb. live weight at three different ages as described in Chapter 9 and illustrated in *Figure 9.2.*

(A) *The effect of the Low plane of nutrition from birth to 16 weeks on the general conformation of the pig is illustrated in *Figure 10.46.* The Low plane pigs retain their juvenile form, have a relatively large*

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head, are leggy, with shallow body and extremely poorly developed hams as compared with High plane ones at the same age. As in lambs (page 483) the restricted nutrition of the Low plane pigs exerts marked differential effects on the relative development by weight of the different joints of the carcass in the direct order of their maturity (*Figure 10.47*); the early maturing head is least affected, followed by shoulders, leg, neck, pelvis, thorax and loin; thus, as in the sheep, indicating the priority claims of early maturing parts for the available

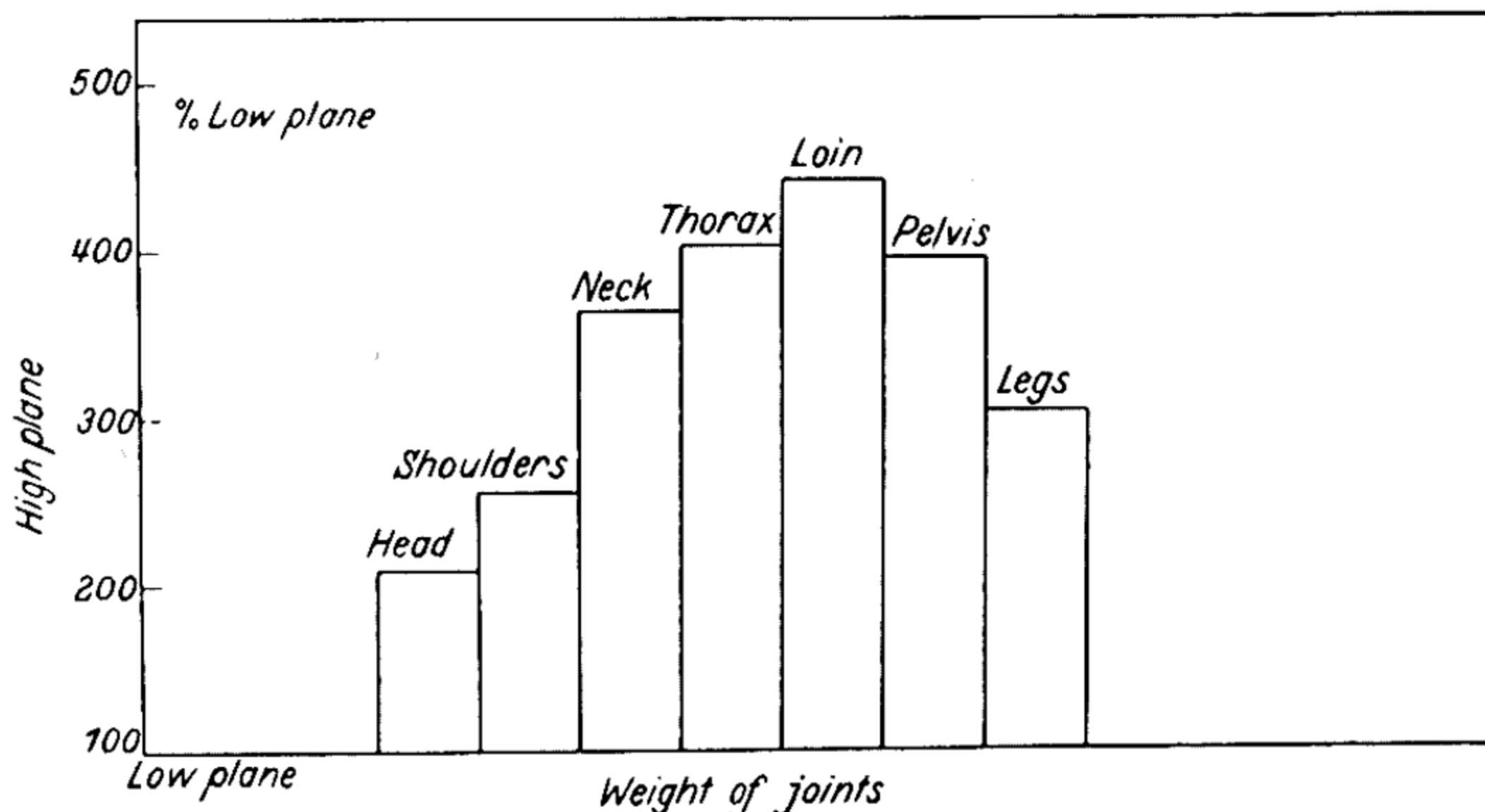


Figure 10.47. Difference in body proportions of pigs at 16 weeks old, fed on high and low planes of nutrition. The weight of each joint in the High plane pigs is shown as a percentage of the weight of the same joint in the Low plane ones. Compare with *Figure 10.29*. (From McMeekan, 1938, by courtesy of *Proc. Amer. Soc. Anim. Prod.*)

nutrients. The different tissues are also differentially affected by the Low plane of nutrition in the direct order of their maturity; the nervous tissue (brain) in the High plane pigs weighs only 111 per cent of this tissue in the Low plane ones, while the corresponding figures for skeleton, muscle and fat are 224%, 291% and 1007% respectively. As in the total carcass, so within each joint the different tissues are differentially affected in the same order, and much more so in the later than in the earlier maturing joints. For the trunk joints this is illustrated in *Figure 10.48*. The subcutaneous fat is proportionately more affected than the earlier maturing intermuscular fat; in the High plane pigs the former weighs 1096% and the latter 83% of the same tissue in the Low plane ones. Within the skeleton, one striking difference is observed between the pig and the sheep in response to restricted nutrition. In both species the Low plane of nutrition has differential effects of similar nature on the development of different parts, while in the pig, at 16 weeks, contrary to what is met with in the sheep in postnatal life, no definite distal-proximal gradient of increasing effects is observed in the appendicular skeleton. In this

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respect the pig at 16 weeks resembles the lamb at birth (*see Figure 10.32*), the short bones of the limbs, like the tarsals and the carpals, being more retarded in development by restricted nutrition than the long bones. This apparent species difference is most likely due to the difference in the physiological age of the new-born of these two species, the pig being born much younger physiologically and not reaching the same physiological age as the lamb at birth until it is several

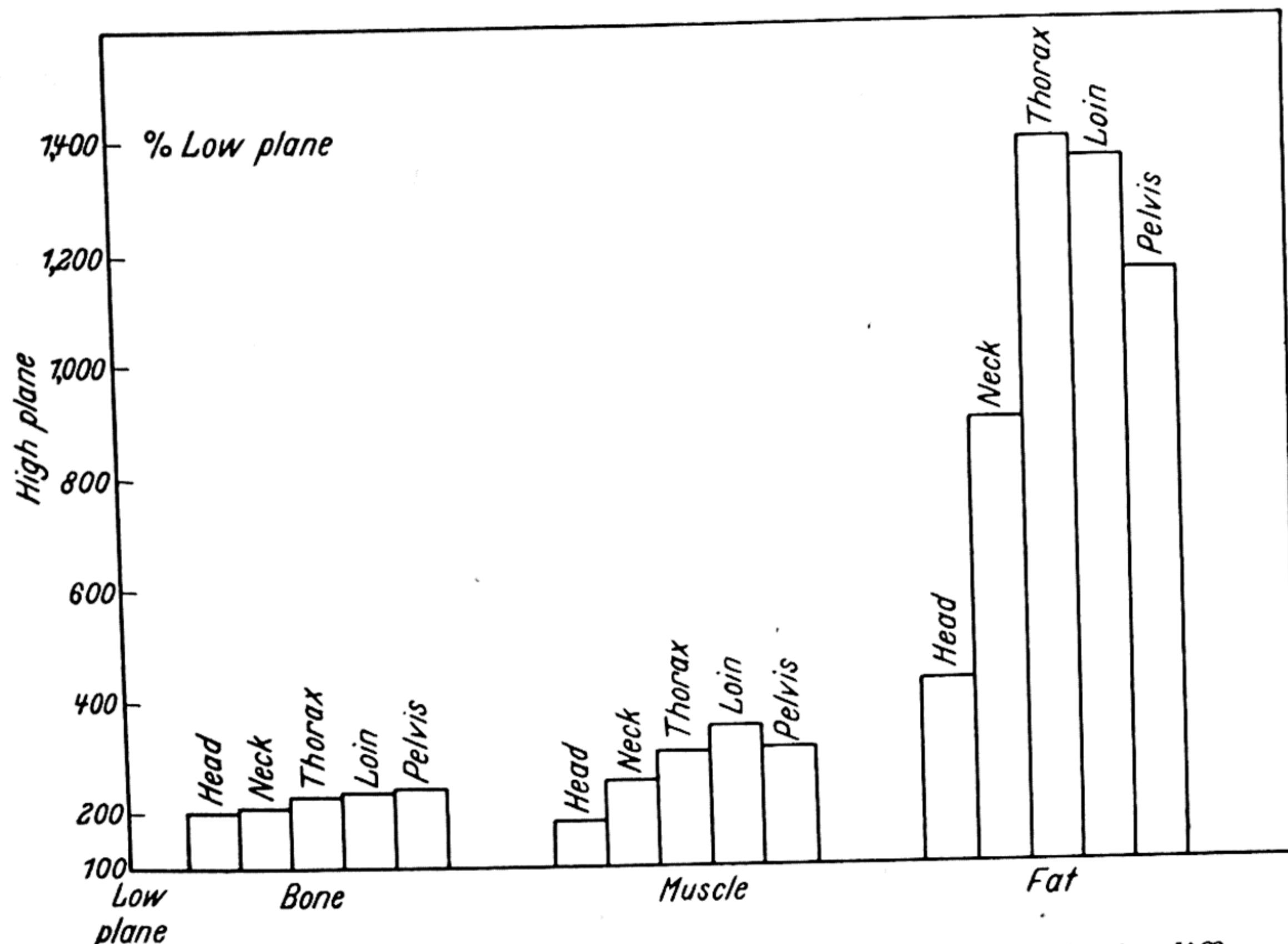


Figure 10.48. Difference in proportions of bone, muscle and fat in different parts of the body in pigs at 16 weeks fed on high and low planes of nutrition. The weight of each tissue in each part in the High plane pigs shown as a percentage of the weight of the same in the Low plane pigs. (From McMeekan, 1940, by courtesy of *J. agric. Sci.*)

weeks old. In general, the organs and offal parts are less affected than the carcass by the Low plane feeding up to 16 weeks, resulting in lower carcass percentage in the Low plane pigs. However, the restricted feeding of the latter causes great differential effects on the development of individual organs and organ groups. As in the sheep the effects are in the main in line with the order of development (*see page 479 and Figure 10.26*). The eyes and brain are least affected, while the thymus gland, uterus, and vagina, and the internal fat depots are most affected. As in the sheep so in the pig, an exception to the general rule is that the late maturing alimentary tract is less retarded in development by a Low plane of nutrition than are the early maturing thoracic organs.

(B) *When comparing the four treatment groups at 200 lb., McMeekan (1940) found that varying the level of nutrition during growth*

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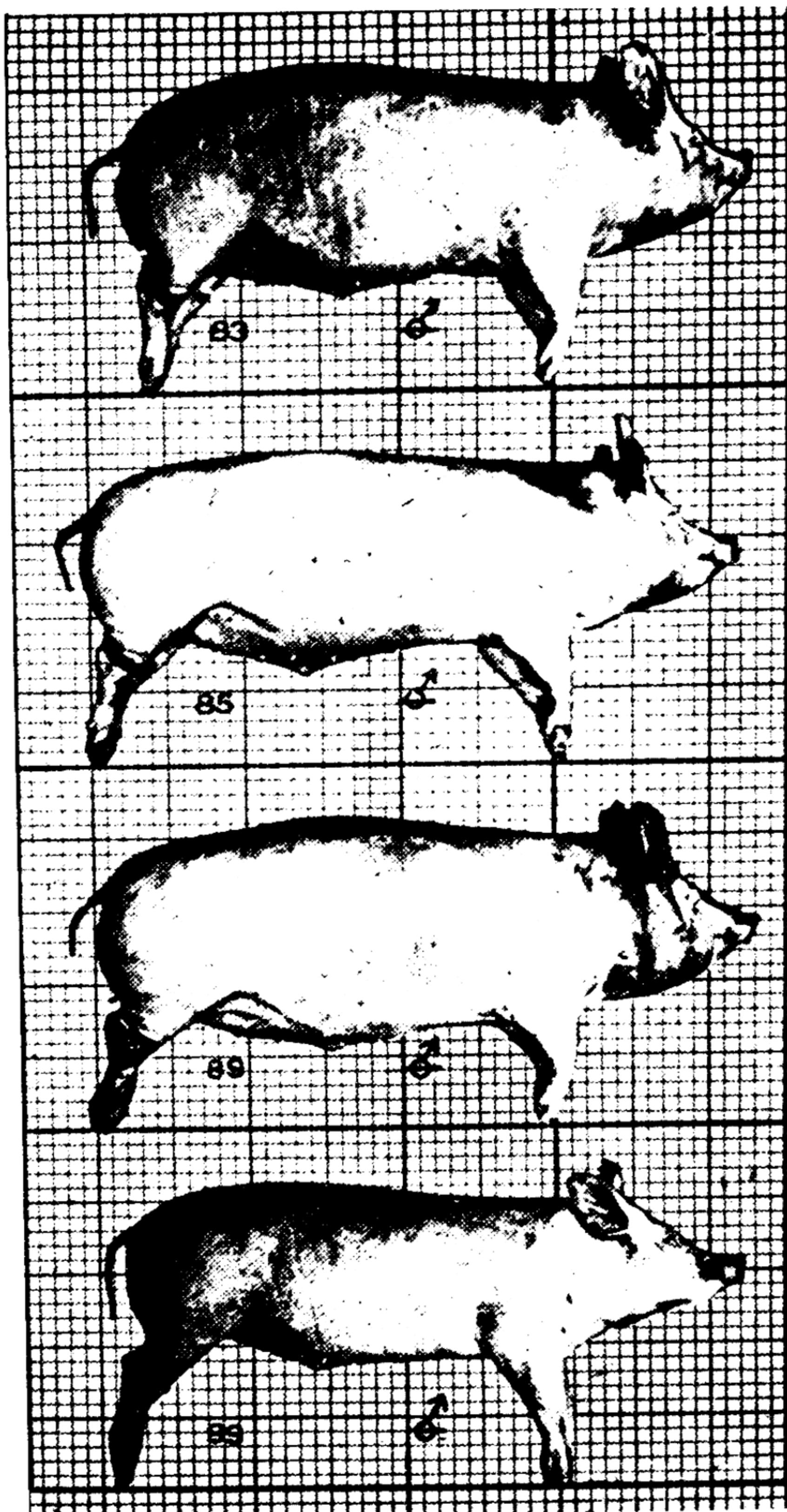


Figure 10.49. The effect of the shape of the growth curve (see Fig. 9.2, Chapter 9) on body conformation in pigs at the same liveweight (200 lb.). All photographs reduced to the same shoulder-trotter height.

- 83. High-High. Quickly grown throughout: 168 days old.
- 85. High-Low. Quickly grown to 16 weeks: afterwards slowly grown: 196 days old.
- 89. Low-High. Slowly grown to 16 weeks: afterwards quickly grown: 196 days old.
- 99. Low-Low. Slowly grown throughout: 315 days old.

(From McMeekan, 1940, by courtesy of *J. agric. Sci.*)

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caused marked differential effects on the conformation and composition of the pigs in spite of their equal body weight. In body form two different types of pigs were produced. As Pálsson and Vergés later observed in the sheep (page 492) the High-High and the Low-High pigs were of much the same type, with relatively small head and short feet, short deep set body, with the late maturing loin-pelvis region well developed, thus being typical of an early maturing breed (see page 461), while on the contrary the Low-Low and High-Low pigs resembled each other, were long bodied, shallow, leggy, with

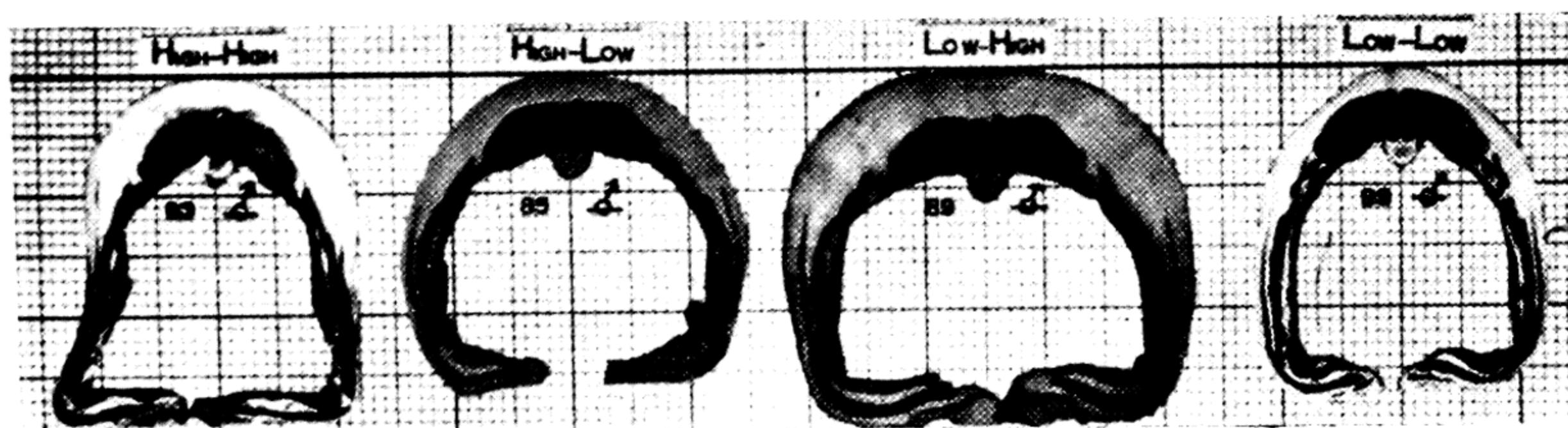


Figure 10.50. The effect of the shape of the growth curve on proportions of tissues at the last rib of bacon pigs at 200 lb. For detail see *Figure 10.49*. All photographs reduced to the same longissimus dorsi muscle length. (From McMeekan, 1940, by courtesy of *J. agric. Sci.*)

long large head and the late maturing loin-pelvis region poorly developed, thus being typical of a very late maturing bacon breed (*Figure 10.49*). Within each type, however, the animals subjected to inadequate nutrition early in life showed relatively greater differences in the characteristics described. The different treatments produced even more striking differences in the relative development of the different tissues, which is illustrated in the cross-section of the carcass at the last rib in *Figure 10.50*. The quantitative development of each tissue in the different treatment groups relative to that in the Low-Low is shown in *Figure 10.51*. The continuous restricted supply of the Low-Low pigs as compared with the continuous high plane feeding of the High-High ones results in much greater development of the earlier maturing skeleton and muscle and much less fat in the former. This is due to the greater competitive capacity of the earlier maturing tissues for the available nutrients, when the nutrient supply is limited. Comparative effects of the different growth curves of the High-Low and Low-High pigs, killed at the same age and weight, are even more striking; the former has much better developed muscle and bone but less fat, while the latter has by far the greatest amount of fat and less muscle and bone than any of the other groups (*Figure 10.51*). The relative effects on the different tissues in the High-Low pigs is similar in nature to those in the Low-Low ones, except that it is less pronounced due to the shorter period of under-nutrition. In the Low-High pigs

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enormous differences in the recuperative capacity of the different tissues are manifest. Recuperative capacity is by far the greatest in the late maturing fatty tissue, because the high plane feeding of this group coincides with the high natural growth intensity of this tissue

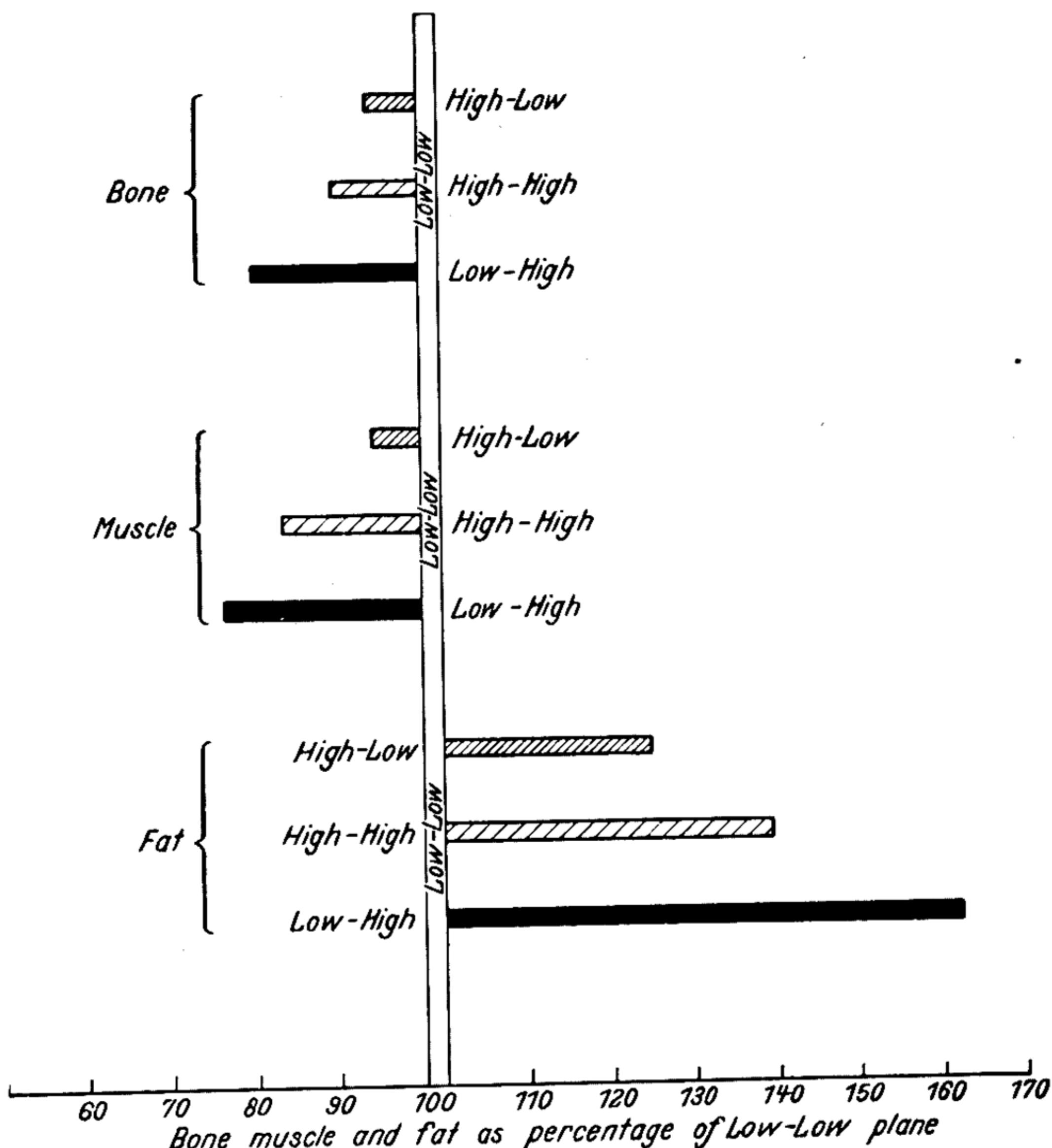


Figure 10.51. The effect of the shape of the growth curve on relative composition of carcasses of 200 lb. baconers. Each tissue in different treatment groups shown as a percentage of the same tissue in the Low-Low group. (From McMeekan, 1940, by courtesy of *J. agric. Sci.*)

at this age. By this age the growth intensity of bone, especially in length and of muscle has much declined, so that these tissues, in spite of their priority claim for available nutrients, need a longer time to make up for the retardation sustained earlier in life.

These experimental results are of great practical importance in the production of high quality bacon. They illustrate the necessity for high plane feeding in early life to exploit in full the high natural growth intensity of muscle at that age, this being followed by a rather limited food supply during the later stages of growth so that bone,

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and even more so muscle, can continue to grow at a high rate for a longer time, while fat is being only slowly accumulated because of successful competition of the earlier maturing tissues for the limited available food supply. Furthermore, this High-Low method of feeding is the most economical from the food conversion point of view (see Chapter 9, p. 402).

In the skeleton the different treatments produce bones of vastly different size and shape. As in the sheep (p. 496) the long bones

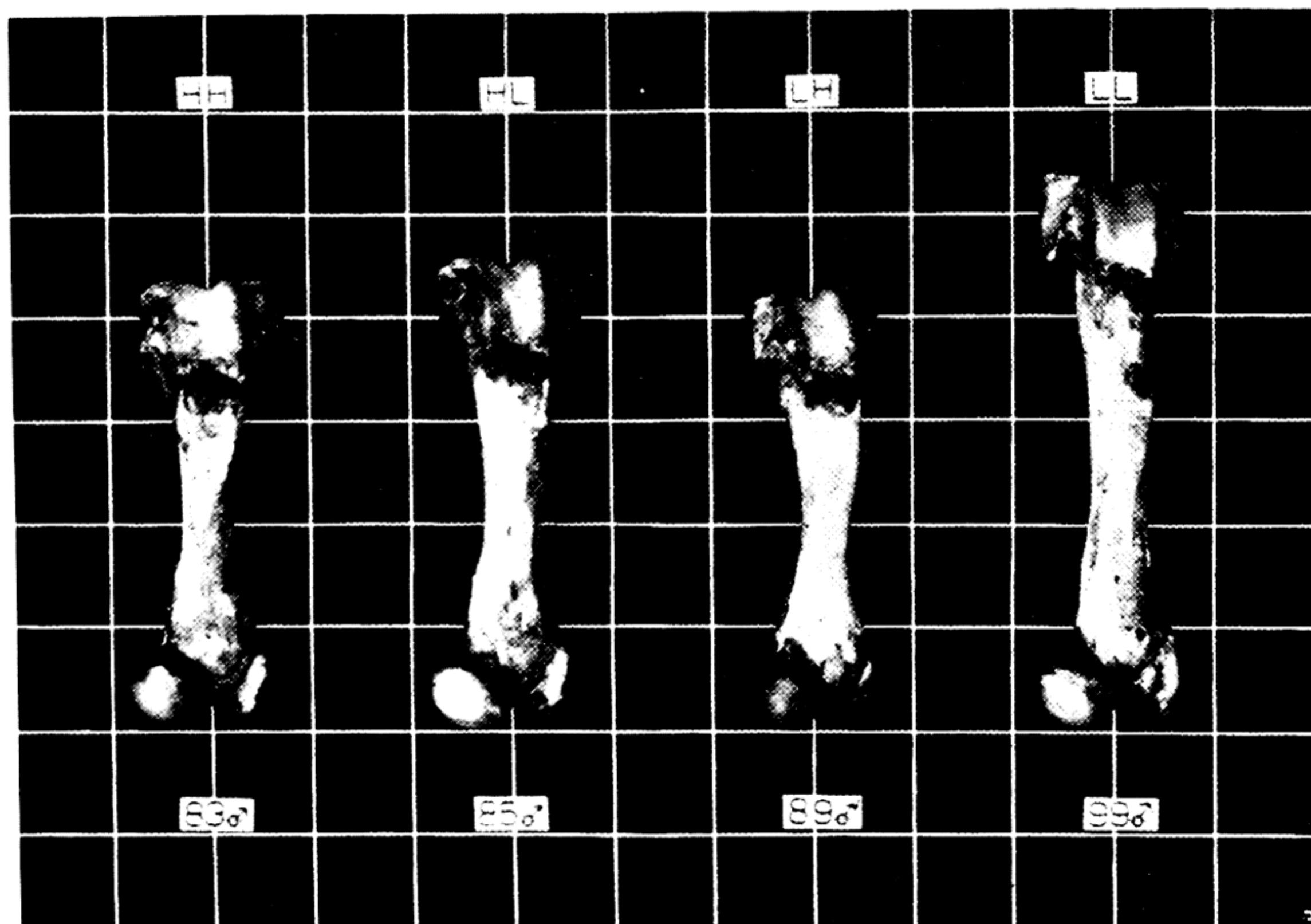


Figure 10.52. The effect of the shape of the growth curve on the size and form of the femur in baconers at 200 lb. Compare with *Figure 10.41* and note the resemblance in bone form in the High-High and Low-High pigs and in the High-Low and Low-Low ones, though still longer in the Low-Low. (From McMeekan, 1940, by courtesy of *J. agric. Sci.*)

are of approximately the same length in the High-High and the Low-High group, being considerably shorter than in the High-Low group and very much shorter than in the Low-Low group (*Figure 10.52*). Even more striking differences are observed in the skull; it is short with a concave or dish-like face in the High-High pigs, more typical of an early maturing breed like the Middle White than of the Large White, while in the Low-Low group it is very long with a straight face and pointed snout, resembling the skull of the wild boar or any very late maturing breed like the Tamworth.

How sub-maintenance feeding of animals, which have not reached mature age or weight, affects the different tissues, organs and body regions has been studied in detail by Pomeroy (1941) in the pig. He used pigs of the same strain as McMeekan (1940, 1941) which were

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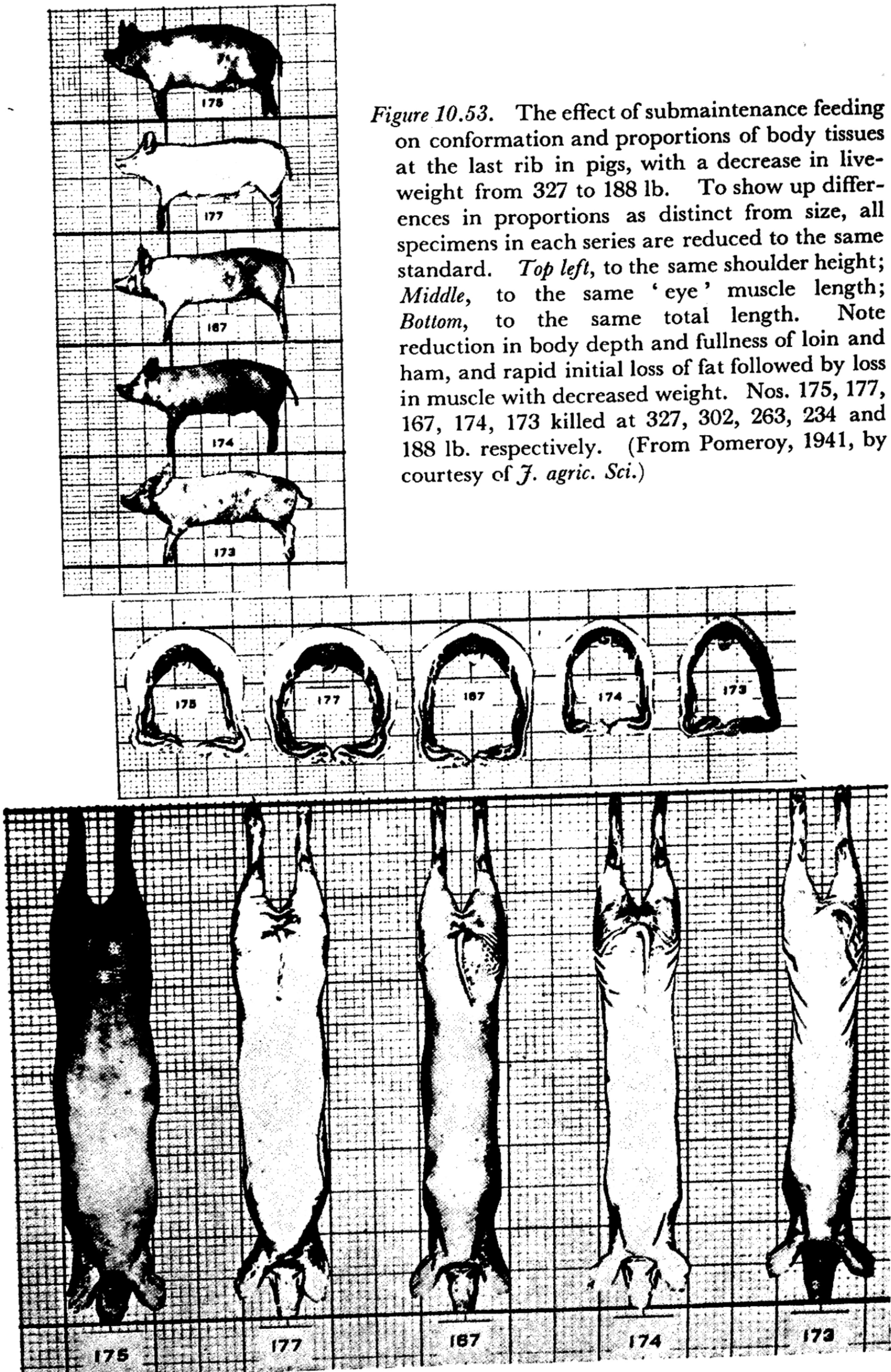


Figure 10.53. The effect of submaintenance feeding on conformation and proportions of body tissues at the last rib in pigs, with a decrease in live-weight from 327 to 188 lb. To show up differences in proportions as distinct from size, all specimens in each series are reduced to the same standard. *Top left*, to the same shoulder height; *Middle*, to the same 'eye' muscle length; *Bottom*, to the same total length. Note reduction in body depth and fullness of loin and ham, and rapid initial loss of fat followed by loss in muscle with decreased weight. Nos. 175, 177, 167, 174, 173 killed at 327, 302, 263, 234 and 188 lb. respectively. (From Pomeroy, 1941, by courtesy of *J. agric. Sci.*)

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fed on a High plane of nutrition until they reached 330 lb., when a control animal was killed, and the remaining animals were subsequently changed on to a sub-maintenance ration, so that they lost steadily in live weight from 330 to 188 lb. during a period of 135 days, individuals being killed at regular intervals. During the sub-maintenance period the general body form changes from being deep in relation to leg length to a shallow and angular form with great reduction in the thickness of the loin-pelvis region (Figure 10.53). The different body tissues are affected in the reverse order of their

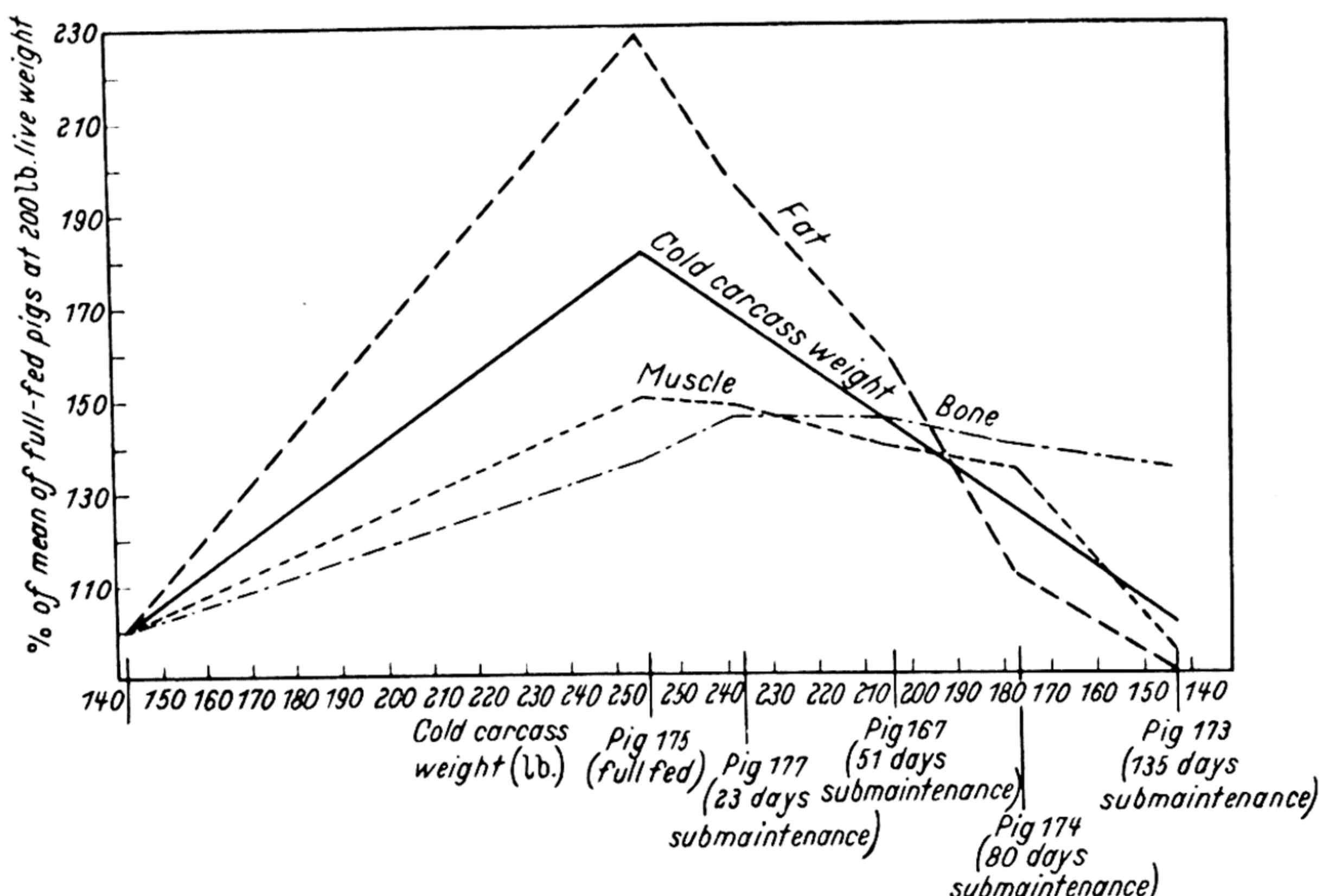


Figure 10.54. The effect of supermaintenance followed by submaintenance feeding on changes in weight of different tissues in pigs. Note the increase in bone weight during the early stages of submaintenance feeding concurrently with rapid decrease in fat. (From Pomeroy, 1941, by courtesy of *J. agric. Sci.*)

development (Figure 10.54 and page 460); fat is lost rapidly throughout, muscle slowly at first, then steadily and at last very rapidly, while bone continues to grow after the other tissues are losing weight (as observed by Waters, 1909 (p. 497), remaining nearly constant for a while but in the later stages slowly losing weight. The earliest maturing nervous tissue continues to increase in weight throughout the sub-maintenance period; it weighed 133.3 per cent of the control after 135 days of semi-starvation, showing its extremely high priority for the limited nutrients in the blood stream (Figure 10.24, page 476). Similarly the eyes continue to gain in weight throughout. The individual internal organs all lose much weight, but to a varying degree, during the early stages of the sub-maintenance period but then either remain constant during the later stages, as in the liver, or lose

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weight very slowly, indicating their greater resistance to starvation than the later maturing body tissues as muscle and fat. The different joints are affected reversely to their order of development, and so is each tissue within the different joints. For example, bone growth ceases first in the loin and last in the head; and the lumbar vertebrae are the first of all skeletal parts to lose weight during prolonged sub-maintenance feeding (Pomeroy, 1941).

Poultry

By controlling the growth curve of chickens normal age changes in their body proportions can be altered in much the same way as in mammals (Wilson, 1952). He studied the effects of rearing chickens on four different planes of nutrition from hatching to 24 weeks, namely, (1) On a High plane throughout (High-High), (2) On a High plane up to 10 weeks followed by a Low plane (High-Low), (3) On a Low plane to 10 weeks followed by a High plane (Low-High), and (4) On a Low plane throughout (Low-Low) using external body measurements. When comparing the four treatment groups at the same age it was found that two types of birds were produced. The High-High and Low-High groups were similar, with the later maturing parts (see page 463) and secondary sexual characters proportionately better developed, while the Low-Low and High-Low ones formed a comparable group exhibiting more infantile body form. When compared at equal body weight, but at different ages, early maturing skeletal measurements, such as the length of head, tarso-meta-tarsus, middle claw and even the relatively late maturing mid-wing, were better developed in the Low-Low and the High-Low groups than in the High-High and Low-High ones, while the late maturing thickness of leg, indicative of muscular development, was better developed in the latter groups.

Growth rate in the higher animals has been described by some authorities (BRODY, 1927; ROBBINS *et al*, 1928; Brody, 1945) as a discontinuous process, *i.e.* the growing period being divided into several well defined age intervals (growth cycles) during each of which growth takes place at a constant percentage rate. This theory has been based on results from averages of a large bulk of growth data in different species. Since, however, growth is so profoundly affected by the plane of nutrition as described above (pages 475-477) it is obvious that the time intervals of constant percentage growth rate may be extended at will by lowering the plane of nutrition, if in fact growth cycles do exist. It seems highly probable that natural growth rate is a continuous process with no well defined breaks, the apparent sharp breaks in the rate of growth observed in many growth studies being rather a result of environmental changes than due to inherent causes. Furthermore, since the plane of nutrition affects the various

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parts and tissues of the body as well as different parts of the same tissue differentially, the theory of a constant specific growth ratio between the growth of any two parts of the animal, formulated by HUXLEY (1924, 1932, 1950) in his heterogonic or allometric equation $y = bx^k$ * and widely used by students of growth, cannot safely be applied to growth in animals of determinate growth (Pálsson and Vergés, 1952).

EVOLUTIONARY CHANGES

The improved breeds of farm animals of today have been evolved from wild ancestors, representatives of which are still surviving, for example, the Mouflon Sheep and the Wild Boar (*Figure 10.55*). During the progress of evolution under domestication the different species have undergone vast changes in body proportions and conformation. The improved breeds have reached proportionally a much more advanced stage of development of the late maturing parts and tissues of the body than the wild ancestral species, the latter resembling more a juvenile form of the improved breeds (see page 438 and *Figures 10.4, 10.55*). These changes in body proportions are a result of selection by the livestock breeder to suit his requirements, often in an artificial environment created and controlled by him. They are at present taking place at a faster rate than ever before, due to our increased knowledge of the physiological factors involved. Under natural conditions the life of wild animals is an everlasting struggle for existence, food supply as a rule being scarce, at least during a period of the year. For survival under such conditions good development of the essential organs, the nervous system, the head and feet is necessary, while the animal does not benefit from great development of the flesh in the late maturing loin-pelvis region; on the contrary this latter results rather in increased nutritional requirements for maintenance and may be a handicap when the animal is moving in search of food or escaping an enemy. Consequently, natural selection has resulted in the survival of animals of the Wild Boar or the Mouflon Sheep type of conformation, with large head and neck, long legs and poorly developed loin and hind-quarters. The livestock producer, on the other hand, keeps his animals for productive purposes, and in case of the meat animals he wants to increase the proportion of carcass to organs and offal, and the relative weight of the most valuable joints, the loin and the pelvis. Therefore he has selected for breeding individuals with relatively small heads and well-developed hind-quarters. This has been done with great success under systems of

* Where y is the size of a part, x the size of the whole body, or whole body less the part, and b and k are constants, the former of no biological significance, it denoting the value of y when $x = 1$, while the latter is the ratio of the specific growth rates of y and x .

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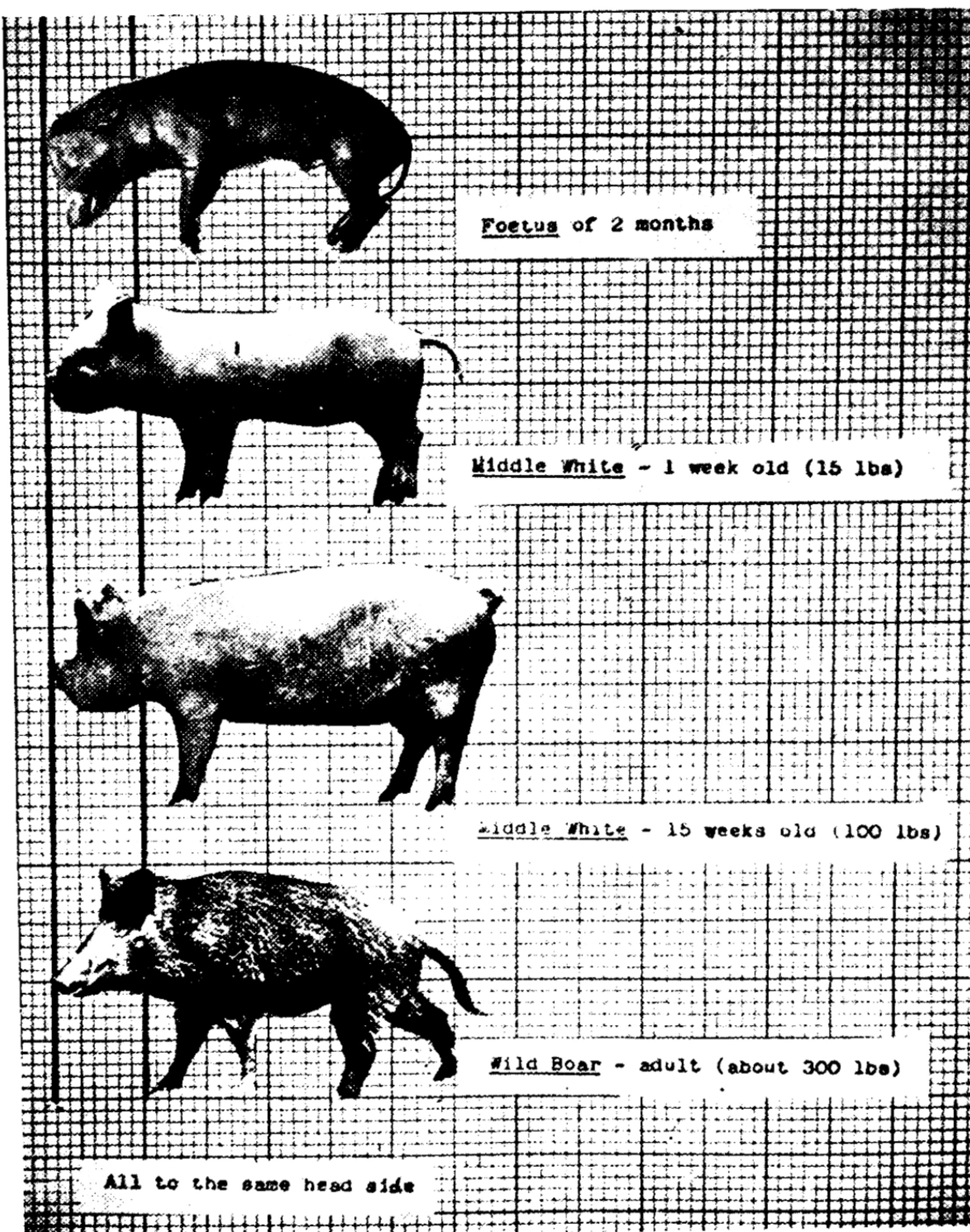


Figure 10.55. Changes in body proportions of the pig with age and evolution. Each animal is reduced to the same head size. As an improved breed like the Middle White grows up, the proportions of loin to head and neck increase greatly, but the Wild Boar grows up without much change in body proportions. *Top*—Foetus at 2 months. *2nd line*—Middle White, 3 weeks old; 15 lb. *3rd line*—Middle White, 15 weeks old; 100 lb. *Bottom*—Wild Boar; Adult; about 300 lb. (From Hammond, 1933-34, by courtesy of *The Pig Breeders' Annual*.)

advanced agricultural practices, where the animals are provided with plentiful food supply the whole year round. On the other hand, in a large number of cases selection for increased production has been a partial or complete failure when practised under primitive farming conditions, where the standard of feeding has not been improved hand

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in hand with selection for increased production. As described above (page 475) recent research work into the interplay of nutrition and development has elucidated why selection for early maturity and advanced development of body proportions is futile unless carried out under optimum nutritive supply, for when reared on a low plane of nutrition, animals of the highly improved early maturing breeds attain only the form of late maturing unimproved ones. Age changes in body proportions in the wild ancestors of our domestic breeds, such as the Mouflon Sheep, are of similar nature as in the improved breeds (see page 437 and *Figure 10.4*). However, evolution based on selection in a suitable environment has resulted not only in these changes proceeding further in the improved breeds, but they do so in a much shorter time chronologically; many of the postnatal changes in body proportions in the wild Mouflon occur prenatally in the improved Suffolk. This early maturity and advanced development of improved breeds is inherited and can be gradually increased from one generation to another, provided the animals are reared in an optimum nutritional environment and those individuals retained for future breeding which attain the highest degree of development in shortest time. HAMMOND (1935, 1936) differentiates between the genetic characters of farm animals broadly as being either gene mutations or developmental characters. The former, responsible for colour, horns, various fancy points and most characters produced by sudden mutations, like the short leg in the Ancon sheep, are usually inherited in a simple Mendelian fashion and are largely or entirely independent of environmental conditions. The latter, which comprise most of the commercial qualities, are gradually evolved by strict selection in an optimum nutritional environment and show blending inheritance, being neither dominant nor recessive and incapable of expressing themselves to any marked extent, although present in the genetic structure of the animal, except in an environment comparable with that under which they were developed.

McMAHON (1943) in a survey of the intensity of inheritance in different characters in a stud flock of Romney Marsh sheep, making more than 1,000 comparisons of each character between parents and progeny, found differences in percentage heritability (Table 10.4).

TABLE 10.4

INTENSITY OF INHERITANCE OF SHEEP CHARACTERS

Character	Average heritability (%)	Character	Average heritability (%)
Head type	25-30	Wool character	14
Breed type	15	Wool count	35-40
Fleshing	13	Fleece weight	10-15

Head type, an early maturing character, is strongly inherited as compared with fleshing, a late maturing developmental character, the latter being much more affected by the plane of nutrition than the former (see page 438 and *Figure 10.6*; McMEEKAN *et al.*, 1943, and HAMMOND, 1947). An estimation of the intensity of inheritance of productive characters in farm animals is of little value unless the investigation is carried out in an optimum nutritional environment; such characters, for example, as good development of loin or high milk yield are incapable of expressing themselves to their genetic capacity in underfed animals and will therefore not show their true heritability. Some authorities (FALCONER and LATYS-ZEWSKY, 1952), however, claim that heritability is higher under a low than a high plane of nutrition. They selected for increased weight in two series of mice, derived from a common stock by random sampling, one series being fed on a high and the other on a low plane of nutrition for generations; the heaviest individuals from each generation were retained for the breeding of the next generation. They found that the progeny of the low plane series had a greater resemblance to their parents in respect to the character in question in the successive generations than did the progeny of the high plane series. This is essentially so because the character selected for has neither possibilities of developing to its inherent capacity in the parents nor in their offspring in the low plane series, so the variability is greatly reduced. It is of no interest to the progressive stock breeder to be able to breed his animals true to a primitive non-productive type by repressing inherent variability by restricted nutrition. On the contrary it is of primary interest to him to be able to see the inherent variability of his breed, which is only possible under plentiful nutritive supply, so that the individuals which are capable of greatest development of the productive characters can be selected for future breeding.

As the male in farm animals is capable of reaching a more advanced stage of development of body proportions (page 466) than the female, greater success can be achieved in breed improvement for meat production by stricter selection of males than of the females. However, as the males are larger and proportionally more retarded in development by under-nutrition than the females, selection of the best males can only be performed where the plane of nutrition is so high that their most valuable late maturing characters can develop to their maximum inherent capacity or "ceiling" level in the shortest time possible. Due to this reason, for example, breeders of cattle under range conditions must continually buy bulls reared and selected under a high standard of feeding, in order to maintain early maturity and high beef quality in their herds. Bulls bred on the range are incapable of exhibiting their inherent genetic capacity for early maturity, so selection from these for breeding purposes would be a

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matter of chance. On the other hand, in such range circumstances, the females are often capable of reaching so high a degree of development of their late maturing characters as to make selection of the earlier maturing individuals possible; this is because of their inherent smaller size, and less capacity for advanced development than the males.

Sheep

Sheep are kept under a wider range of environmental conditions and in some cases in an environment more similar to the haunts of their wild ancestors. Consequently different breeds vary enormously in evolutionary development, from semi-wild types, not differing much from the wild Mouflon, to some of the most highly developed meat animals like the Down breeds of Britain (*Figure 10.4*); the variation is much greater in the late maturing loin-pelvis than in the earlier maturing joints, it being least in the thorax (Hammond, 1932a; HIRZEL, 1939; Pálsson, 1939, 1940). All the improved mutton breeds have been developed where plentiful food supply could be provided throughout the year. Some of these breeds are large (Border Leicester, Suffolk) and even though early maturing for their size (page 457) require either a longer time or a more abundant food supply to reach desirable body proportions than smaller breeds (Southdown, Ryeland). In recent years with ever increasing demand for young lambs of 26–36 lb. dressed carcass weight (*see* page 529 and *Figure 10.56*) the small breeds have been in favour, and selection for reduced size has been practised to further increase early maturity, for the small sized lambs can in a short season attain the desired proportional development of the late maturing parts and tissues of the body before the carcass weight exceeds the optimal limit, whereas lambs of the larger breeds fail to do so. Increased bone growth in thickness is directly associated with breed improvement for increased meat production and early maturity while the reverse is true for bone growth in length (NATHUSIUS, 1880; Hammond, 1932a; Pálsson, 1939, 1940). In semi-wild breeds, like the Soay and Shetland, bone growth in thickness is inhibited as compared with improved mutton breeds like the Hampshire and Suffolk (*see Figure 10.34*). This is best seen in the forecannon. Pálsson (1939, 1940) found that short forecannons with a thick shaft and fine, light extremities are associated with early maturity and good development of muscle and fat, whereas long cannons with a slender shaft and coarse, heavy extremities are indicative of late development and inferior carcass quality. There is a correlation between a short and broad face and short and thick limb bones. This is of practical use in judging; a short broad head and short thick cannons with fine extremities may be used as indicative of early maturity and desirable meat form. On the other hand, a sheep which has been reared on a low plane of nutrition cannot be

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correctly judged by its appearance for regardless of its genetical constitution, it will invariably resemble in bone form and conformation a late maturing unimproved individual (see page 487). The ideal mutton sheep has short neck and long trunk (Hammond, 1932a; Pálsson, 1939, 1940) and selection for these have long been practised

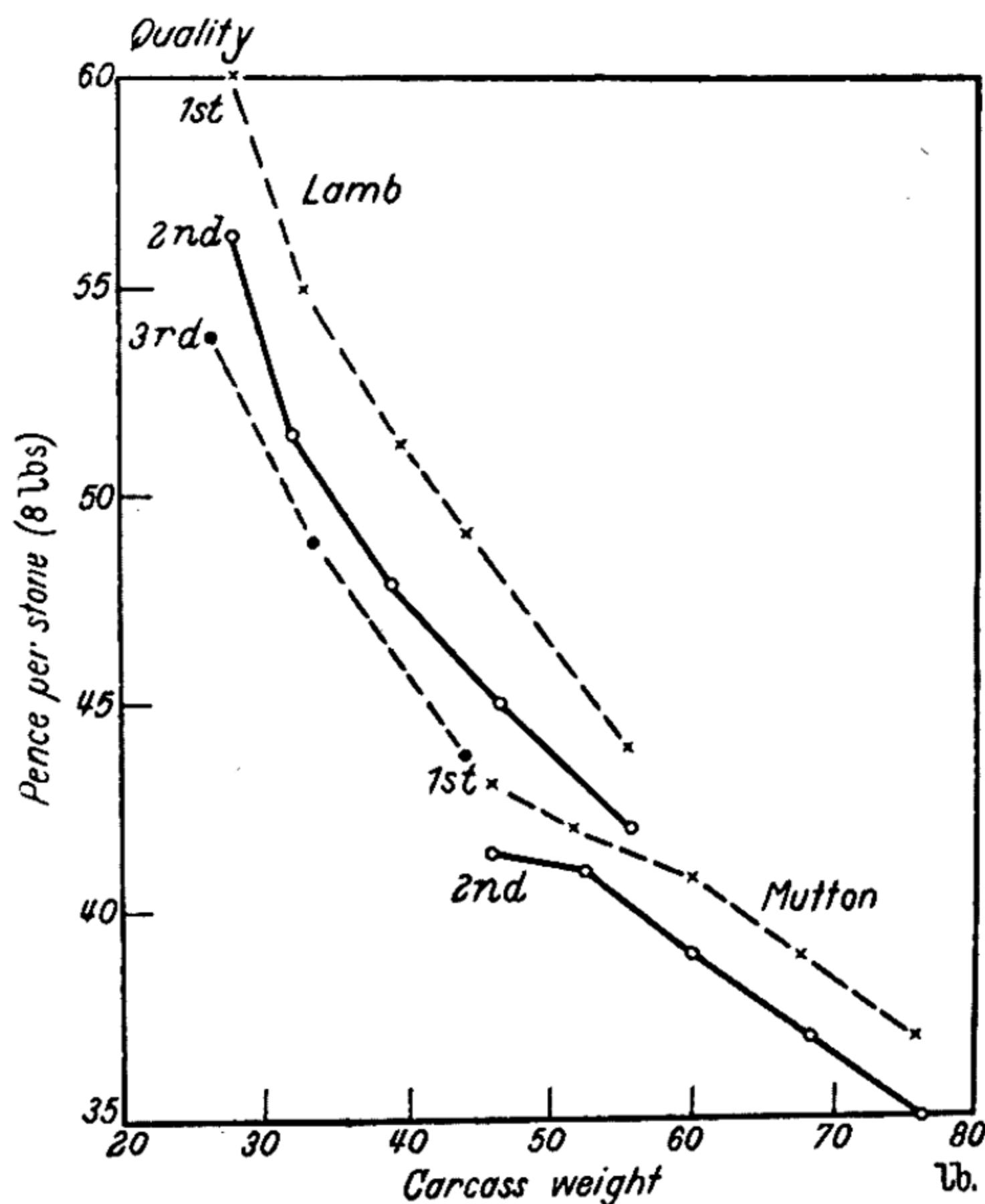


Figure 10.56. Influence of carcass weight and quality on prices of imported (Argentine) frozen mutton and lamb in the London market, Feb., 1937. (From Hammond, 1937, by courtesy of *National Sheep Breeders' Assn.*)

by sheep breeders. As the number of vertebrae and ribs varies in sheep this change in relative length of the body regions can be more easily achieved than otherwise would be possible. Pálsson (1939, 1940) found variation in the number of vertebrae in all parts of the vertebral column, the total number varying from 30 to 32, excluding the caudal vertebrae. Even the cervical vertebrae which are supposed to be seven in all mammals are only six in some sheep. The number of rib pairs varies from 12 to 14 in sheep. The occurrence of six cervical vertebrae is most frequent in short-necked breeds like the Southdown and that of 14 pairs of ribs in the large long-bodied breeds such as the Suffolk and the Oxford. Whether the deviation from the normal number of vertebrae (31) is evolutionary or takes place by sudden mutations is uncertain; in some cases, however, vertebrae are met with, which are intermediate in form between those of one region

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and another, rather indicating evolutionary changes which may be encouraged by selection (Pálsson, 1939, 1940).

Cattle

As with sheep so the early maturing highly esteemed beef breeds of today are evolved from primitive types by directive selection in an environment of plentiful food supply. Similar changes in body proportions and early maturity have taken place in beef cattle as in sheep. The head and legs have been reduced in size while the late maturing loin-pelvis region has been proportionately increased and the trunk as a whole has been increased in depth and width, more so in the hind than in the fore quarters. These evolutionary changes in Hereford cattle are illustrated in *Figure 10.16*. The adult bull of 100 years ago resembles more in conformation one of 13 months old than the adult one today (compare Nos. 15, 3 and 5, *Figure 10.16*). The modern dairy breeds which have been developed by directive selection not for beef but for high butter fat and milk yield, still retain more of the primitive form. Contrary to the beef breeds, the dairy breeds have long heads and legs, and do not proceed so far in the postnatal development of the late maturing loin-pelvis region as the beef breeds (see page 458). A $5\frac{1}{2}$ -years-old Friesian bull has much the same body proportions as the 14-months-old Beef Shorthorn bull, and the 18-months Aberdeen-Angus bull is even better developed than the $4\frac{1}{2}$ -years-old Dairy Shorthorn and the $5\frac{1}{2}$ -years-old Friesian bull (Hammond, 1935).

Horses

The natural evolution of the horse is from a small short-legged marsh-living animal about the size of a dog (LOOMIS, 1926) to a long-legged one equipped for speed on dry ground (*Figure 10.57*). These evolutionary changes in body proportions are repeated during the course of foetal development in the Welsh pony today (*Figure 10.57*). The three-months foetus of the Welsh pony has much the body proportions as the primitive Eohippus and the Welsh foetus of seven months resembles that of the Merychippus (Hammond, 1935). Thus both in evolution during time and in the foetal development of the individual today, there is an increase in the proportions of the length of leg, fitting the horse for speed. The postnatal changes in body proportions in the Welsh pony, however, differ from the prenatal changes in that the body becomes deeper and thicker so that the head and legs become smaller in proportion to the trunk in the adult than in the new-born foal (see page 519). Evolution of the horse under domestication has been along two different lines, for speed and for draught. In the Thoroughbred, which has been bred for speed, leg length has been increased in proportion to the depth of body, *i.e.* it

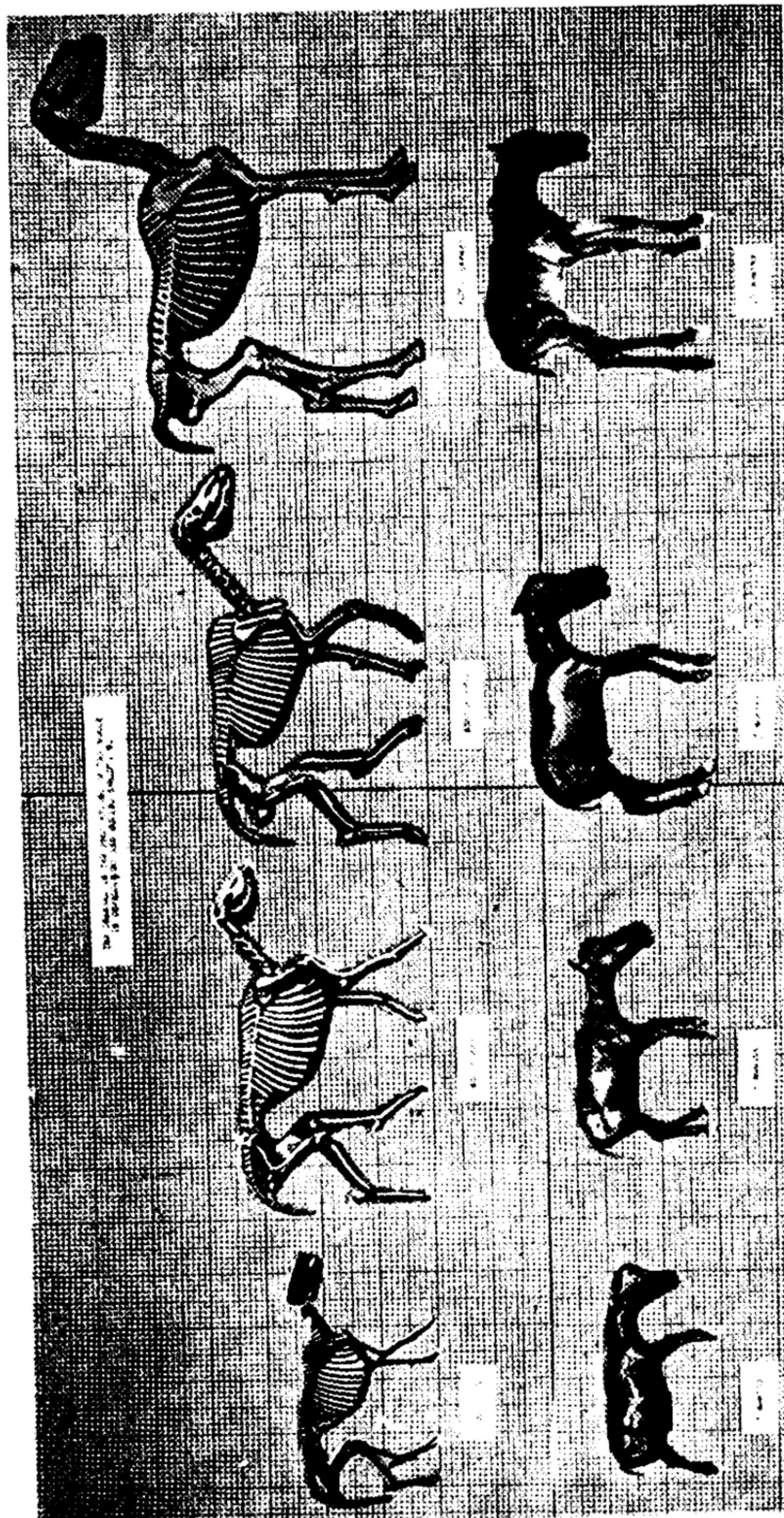


Figure 10.57. The changes in the proportions of the body in the horse during evolution and in the development of the individual. In order to show the changes in proportions, all the photographs have been reproduced to the same cranium (eye-ear) length. The changes in proportions during foetal life are parallel to those which have taken place during evolution. Reading from left to right:

Top line—Evolution: Eohippus; Mesohippus; Merychippus; Equus (Arab).

Second line—Development (Welsh Pony): Foetus 3 months; 5 months; 7 months; 10 months.

Third line—Development (Welsh Pony): Foetus 11 months; 2 weeks after birth; 9 weeks; Adult.

Bottom line—Evolution: Thoroughbred (an extension of second line); Suffolk draft horse (an extension of third line). (From Hammond, 1935, by courtesy of *Emp. J. exp. Agric.*)

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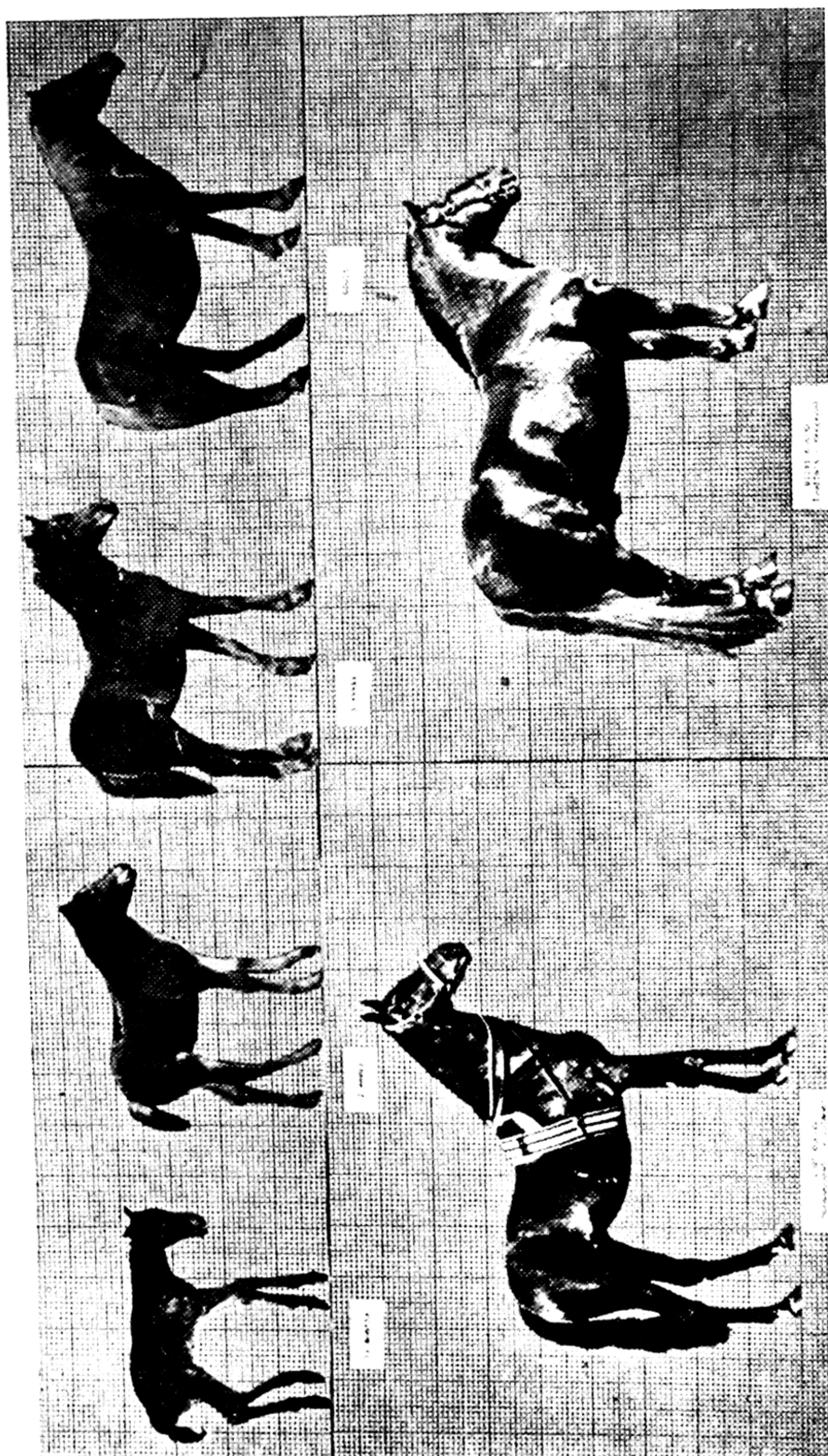


Figure 10.57 (continued from previous page).

has been continuing the main evolutionary changes of the horse and those which occur during foetal development. On the contrary the heavy draught horse has been developed by selection for increased weight and strength, its evolution consisting of an extension of the postnatal changes occurring in the Welsh pony and is comparable with the development of the mutton breeds of sheep and beef cattle (*Figure 10.57*).

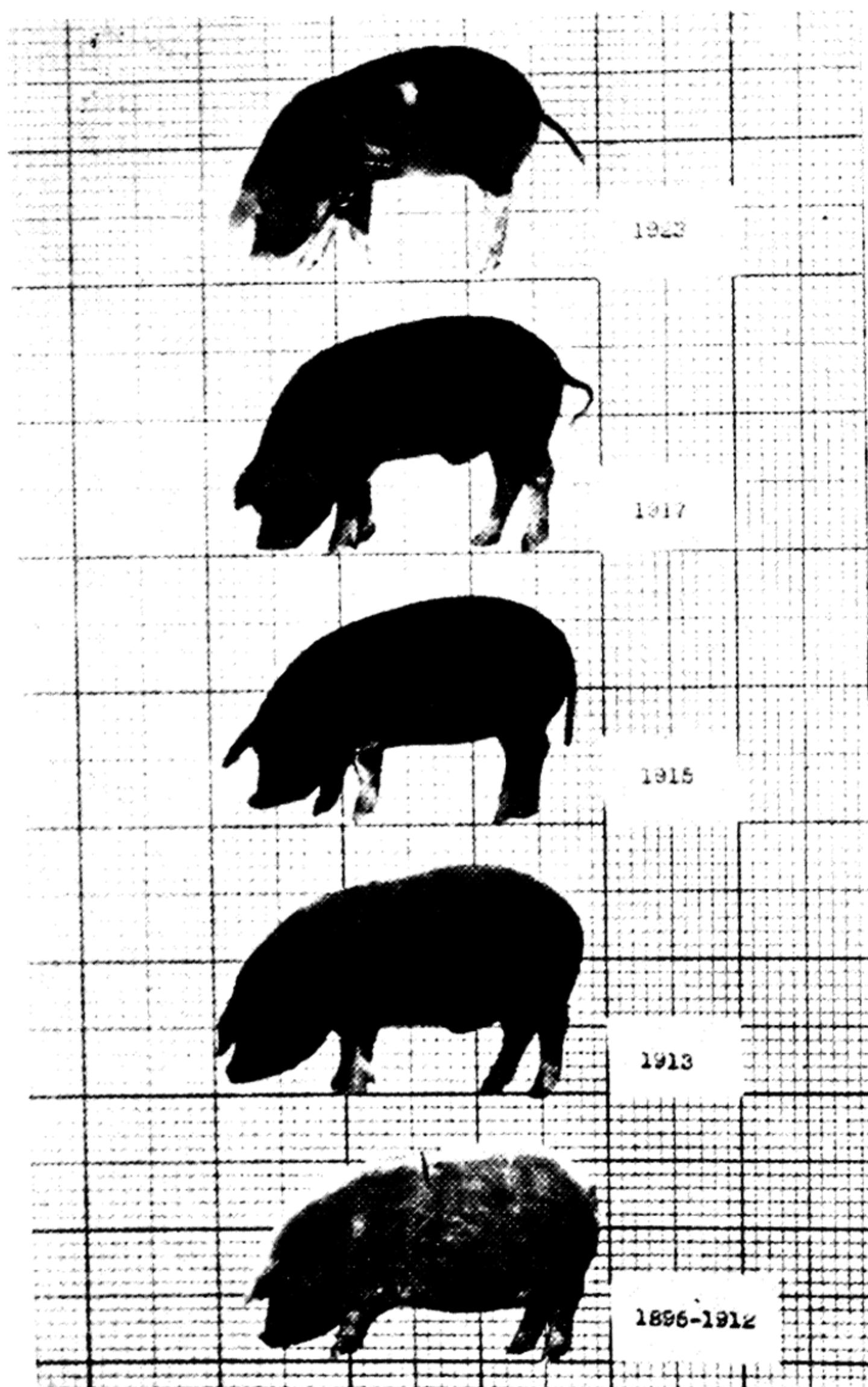
Pigs

The evolutionary changes in the pig under domestication from the Wild Boar type to the early maturing pork breeds of today are of a similar nature and have followed the same lines as in the mutton breeds of sheep (*Figure 10.55*). The pig can be moulded to suit the breeder's requirements by selective breeding and nutrition even more easily than other species of farm animals. No farm animal has evolved to such a high degree of proportional development of its latest maturing body parts and tissues as the lard type of pig, the Poland-China in U.S.A. and the Mangalitza of Hungary and Roumania. This has been done by selection for short bone and light frame in general under a system of plentiful food supply in the maize producing areas in these countries. In the U.S.A., with decreasing demand for lard and increasing demand for bacon with a high proportion of muscle, the evolution of the Poland-China pig has been reversed from the early maturing lard type to the late maturing bacon type, by selection for larger size and lowering the plane of nutrition prior to slaughter (*Figure 10.58*). However, as described above (page 503 and *Figures 10.49* and *10.50*), much the same changes in body proportions can be brought about in litter mates of the same inbred strain of Large Whites by changing the plane of nutrition only.

Progeny testing based on carcass measurement, such as body length and thickness of belly and back fat, is an efficient method to hasten the evolution of bacon pigs with the most desirable body proportions (*Figure 10.59*). It has been used with great success in countries like Denmark (CLAUSEN, 1938-39, 1952), Sweden (BENGTSSON, 1938), Norway (BERGE, 1936), Holland (RIJSSENBECK, 1937) and Canada (STOTHART, 1937). In pigs, as in sheep, there is considerable variation in the number of vertebrae and ribs, the number of rib pairs varying from 13 to 17 (SHAW, 1929-30; TUFF and BERGE, 1936; McMEEKAN, 1940, 1941). Tuff and Berge (1936) found a high correlation between body length and the number of vertebrae and ribs in pigs; for each additional rib the body length in pigs at bacon weight increased by 1.2 cm. Furthermore, BERGE (1948) found the variation in the number of vertebrae in pigs to be inherited, the type of inheritance being intermediate and the coefficient of heritability being high (0.74). Knowing this, selection for increased number of

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vertebrae should be the most efficient method for increasing body length in pigs.



*Figure 10.58. Changes in body proportions which have taken place by selection in the Poland-China pig as the demand for lard decreased. From bottom upwards—1895-1912; 1913; 1915; 1917; 1923. (From Hammond, 1932b, *J. Royal agric. Soc.*)*

QUALITY IN MEAT

The concept of meat quality varies to some extent between countries as well as between markets within a country, and changes from time to time (Hammond, 1932a; Hammond and Murray, 1934; Hirzel, 1939; Pálsson, 1939, 1940; McMeekan, 1940, 1941; STARKE, 1951). However, numerous factors contribute to meat quality in general; the most important are (1) *The composition of the carcass in terms of bone, muscle and fat*: The percentage of muscle should be high and that of bone low, and just sufficient fat to prevent the meat from undue

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drying in storage, transit and cooking. (2) *The relative development of different joints:* The parts of the carcass containing the thickest musculature, such as the loin, legs and pelvis should make up a high proportion of the carcass, while the neck and thorax should be relatively light. (3) *The size and shape of the joints:* The consumer's demand is for a small compact joint of relatively light weight. The

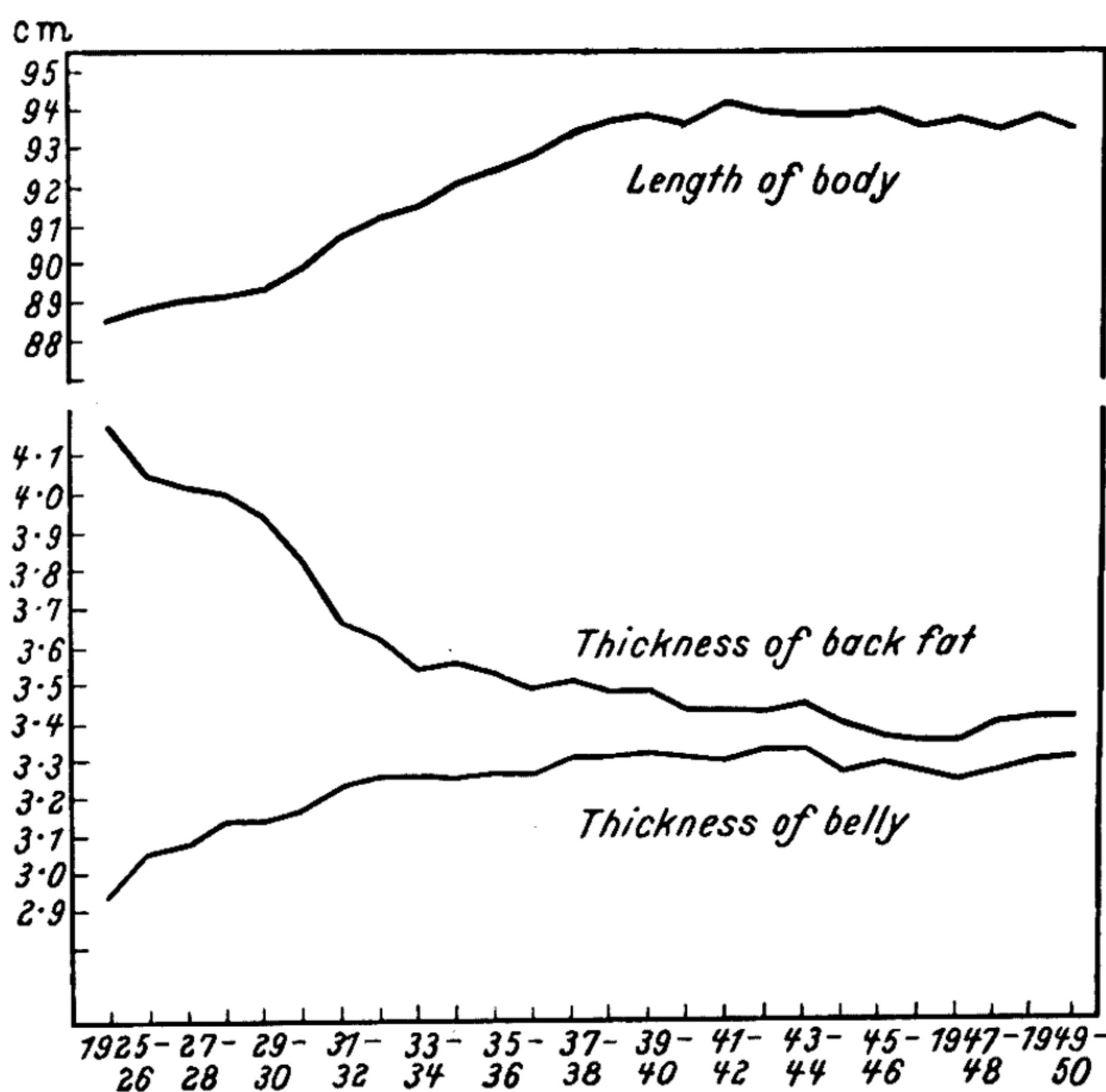


Figure 10.59. The effect of selection on changes in length of body, thickness of backfat and thickness of belly (cm.) in the Danish Landrace pig at bacon weights in the years 1926–1950. (From Clausen, 1952, by courtesy of *The Pig Breeders' Gazette*.)

bone should be absolutely short, so that for any given weight of joint the flesh covering the bone becomes thick. After cooking such a joint gives thick slices of succulent meat in contrast to a long joint with a thin flesh covering which is liable to dry up in cooking. (4) *The distribution of fat:* A high proportion of subcutaneous fat to intermuscular fat is desirable and the former must not be patchy but evenly distributed over the whole surface of the carcass. Joints having a high percentage of intermuscular fat, such as the neck and thorax, fetch a lower price than the legs and loin which have a low percentage of intermuscular fat. (5) *The texture, flavour and colour:* The muscle should be finely grained, tender and light to bright red in colour. The fat should be firm and white as yellowish fat is objectionable to

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the eye, and soft fat becomes rancid easily due to oxidation of unsaturated fatty acids. (6) *Chemical composition of muscle and fat*: A low water content in both tissues, a high fat content in the muscle (marbling fat) and a low percentage of unsaturated fatty acids in the fatty tissue is desirable. Marbling fat increases tenderness and palatability, especially in coarse grained meat of large and/or old animals, while unsaturated fatty acids soften the fat and reduce the keeping quality of the meat. All these factors are influenced by the age, sex, plane of nutrition, and breed of the animal. The influence of age is of a similar nature in the different species; there is, however, a considerable species difference in the influence of sex and nutrition on some of the factors affecting meat quality. Increase in carcass weight has beneficial effects on meat quality until the animal has reached the ideal degree of fatness, for not only does the proportion of edible meat to bone increase during the postnatal stages of growth, but so also do the proportions of the most valuable late maturing joints in the carcass (see pages 479-489). In all species at birth the muscle is fine grained and tender but lacks flavour, whereas with increased age it becomes coarser, tougher and stronger flavoured. The ideal age for slaughter is when the muscle has not yet become too stringy or too strongly flavoured; it is therefore of utmost importance in meat production to feed the animals well so that they reach a desirable state of fatness while still relatively young. During the early stages of foetal life, growth in muscle takes place both by increase in the number of muscle fibres and by their increase in size. Some time before birth the muscle fibres cease to increase in number but at what stage is not yet known. The diameter of the muscle fibres increases with age (Figure 10.60 and Joubert, 1955). In some muscles of the body, such as the *vastus externus*, the muscle fibres grow much larger in diameter than in others, such as the *gracilis* (Figure 10.61; Hammond, 1932a). Joubert (1955) compared the postnatal changes in muscle fibre size of three muscles in sheep, the *longissimus dorsi*, *gastrocnemius* and *rectus femoris*. He found the fibres in the *gastrocnemius* to be largest at birth and maturing earlier than in the *rectus femoris*. The fibres in the *longissimus dorsi* showed the greatest postnatal increase in size, being smallest at birth and nearly the largest at maturity. The muscle fibres are arranged in bundles, so that growth in muscle fibre diameter results in an increase in the size of the muscle bundles; as a result the meat becomes coarser grained with age (Figure 10.60; Hammond, 1932a). For the same reason muscles containing fine muscle fibres such as the undercut are finer grained and more tender than others such as the rump muscles of the same carcass. For the same reason also small species and breeds of animals have finer grained muscles than larger ones, thus giving more tender meat. The tenderness of muscle is also affected by the connective



Figure 10.60. The effect of age on the diameter and thus the grain of muscle fibres of Suffolk rams. Sections through the fibres of semi-membranous muscle of a lamb at birth (*top*) and at 5 months old (*bottom*). (From Hammond 1932a, by courtesy of Oliver and Boyd.)

tissue, the extra-cellular protein forming a soft skeleton surrounding and supporting the muscle fibres by thin strands and the muscle bundles by thicker layers, thus giving meat its structure and firmness. The connective tissue makes up a higher percentage of the muscle weight in the new born than in the mature animal (BATE-SMITH, 1942).

However, with age and exercise its collagen content increases and so its toughness. The amount of connective tissue varies greatly in different muscles of the animal, it being for example very high in the fore shank but low in the longissimus dorsi muscle (MITCHELL *et al.*, 1928-29). During fattening fat is deposited in the connective tissue



Figure 10.61. The difference in coarseness of grain of different muscles in a Suffolk ram at 5 months old. *Left*—The gracilis, fine grained. *Right*—The vastus externus, coarse grained. (From Hammond, 1932a, by courtesy of Oliver and Boyd.)

between the muscle bundles (marbling fat) which tends to split up the latter and thus increase tenderness of the meat. This is important in old animals of all species, in large animals with coarse grained meat, and cattle at relatively young age, whereas it is of little importance in pork and lamb. The hanging of meat, which causes the connective tissue binding to soften, and beating meat against the grain with a chopper also improves the texture of meat (HAMMOND, 1942).

The intensity of flavour of muscle is closely associated with its colour (Hammond, 1932a). The red colour of meat is mainly due to myoglobin (often referred to as muscle haemoglobin) a protein very similar in properties to blood haemoglobin. It is red in the presence of oxygen and purple brown in its absence. The reduced form can oxidize to methaemoglobin, which gives to meat an unpleasant brown colour (Bate-Smith, 1942). For each type of meat there is an optimal colour. The dark coloured flesh of bulls, for example, is too highly flavoured, while the pale flesh of very young animals, bobby calves, lacks flavour. Colour scales have been produced so that the optimal colour can be judged (Hirzel, 1939). The myoglobin content of

muscle, and so its flavour, increases with age and exercise and so the muscles of game animals such as grouse and deer are darker and more highly flavoured than those of the domesticated fowl and sheep. This difference is also to be found between the various muscles of the same animal. Thus the leg muscles of the chicken are darker than the breast muscles and in the leg of mutton the extensor pedis muscle, which is continuously functioning to keep the leg in an upright position, is dark in colour, whereas the semitendinous muscle, which is only occasionally brought into use, is pale. Sex affects the colour of muscle, males having darker muscles than females, while castration reduces the colour (Hammond, 1932a; Hirzel, 1939). Absence of iron from the food, as in milk-fed veal, decreases the colour of muscle, whereas turning the animals out on grass increases it. Animals reared on a low plane of nutrition have darker muscles than those reared on a high plane (Trowbridge *et al.*, 1918; Bull *et al.*, 1930; McMEEKAN, 1940, 1941; Pálsson and Vergés, 1952).

Normally living muscle contains some 1 per cent glycogen, which, however, varies somewhat between species as well as between muscles of the same animal. On death, glycogen is rapidly broken down to lactic acid with the result that the *pH* of the muscle decreases from 7.5 to 5.7 provided sufficient glycogen is present; it decreases by 1 *pH* for 0.5 per cent of glycogen broken down. This enhances the keeping quality of meat and is a factor in causing rigor mortis. The glycogen reserves of muscle are depleted by fatigue, so that meat from animals which are killed in a fatigued state does not acquire the low *pH* required for proper rigor mortis and high keeping quality. Meat with a *pH* above 6.2 remains flabby and has very poor keeping quality.

The state of fatness and the rate at which it occurs is the most important single factor affecting meat quality. During fattening on a high plane of nutrition more fat is added to the late maturing carcass than to the offal parts which are early maturing, so the carcass percentage goes up. Thus the carcass percentage is a guide to the composition of the carcass, provided other factors such as breed and fill of stomachs are equal (CALLOW, 1944). For bullocks, for example, Callow (1944) found that for every increase of 1% in carcass percentage, the fatty tissue of the carcass increased by 1.43%, the edible meat increased by 1.23% and the bone decreased by 0.28% (all expressed as percentage of the live weight). The amount of marbling fat in the iliospinalis muscle in bullocks increases from 11.8% for those giving a carcass percentage of under 53 to 20.4% for those giving a carcass percentage of over 57 (McKenzie and Marshall, 1918). The amount of chemical fat in the adipose tissue increases with the percentage increase of fatty tissue in the carcass. Young animals and late maturing ones, as compared with older and/or earlier maturing animals, however, contain less chemical fat in their fatty tissue than would be

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expected from their state of fatness (CALLOW, 1947). Fat is firmest in sheep, followed by cattle, and softest in pigs, and it is only in the latter that soft fat is a serious problem. The degree of firmness varies with the fat deposit; in all species the subcutaneous fat, in pigs the outer layer, is softest and the kidney fat firmest. The higher the temperature of the part in which the fat deposits occur the higher the melting point of the fat, other things being equal. The percentage of unsaturated fatty acids as measured by the iodine number is affected by the rate of fattening and by age (CALLOW, 1935; McMeekan, 1940, 1941). For young pigs the iodine number is highest and their fat is softest in the late maturing posterior region of the body, while the situation is reversed at later ages when the rate of fat deposition becomes higher in the late maturing parts. Similarly low plane pigs have softer fat than high plane ones. Both in pigs and sheep the iodine number decreases with age (McMeekan, 1940; Pálsson and Vergés, 1952). There is, however, a great difference between these two species; the plane of nutrition or the rate of fattening has a much greater influence on the iodine number of the fat than age in pigs while the reverse is true for sheep (McMeekan, 1940; Pálsson and Vergés, 1952). The quality of the food fed has an effect on the firmness of the fat deposited, especially in pigs. If the ration for pigs contains soft fats or oils, such as whale oil, the pigs assimilate and deposit a considerable proportion of these unchanged in their fatty tissues and particularly in the outer back-fat layer (GARTON *et al*, 1952). Fat formed from carbohydrates gives as firm a fat as the species or the particular depot is capable of producing.

In some species a yellow colouring matter from the green colouring matter of the feed is put on with the fat; in cattle it is carotene and in poultry xanthophyll. In cattle the depth of colour varies with the breed. The colour deepens with age (HIRZEL, 1935, 1939), being, for example, of much higher intensity in old cows than in young cattle. When the animal goes back in condition and uses up its fat reserves, for example, for milk production, the colouring matter remains and becomes concentrated. Thus the fat of old animals which have had periods of rise and fall in condition during their lives, is usually of deeper colour than in those which have been kept in a thriving condition throughout their lives (Hammond, 1952a). Stall fed cattle on roots and concentrates usually have paler fat than grass fed ones due to the high chlorophyll content of grass. As a rule sheep have white fat; occasionally, however, sheep are found which have a yellow fat, a most undesirable character. ZOPHONIASSON (1934) in Iceland sheep has found this to be inherited in a simple Mendelian fashion, the character being recessive. The fat in pigs is white except in cases where special substances are fed.

Besides elucidating the physiological principals governing growth

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and development and how these affect meat production in general, an important practical aspect of growth studies in farm animals has been to develop systems by which carcass quality in different species may be evaluated on factual grounds by carcass measurements. By the use of a simple score card system based on carcass measurements which have been found to be highly correlated with meat quality, the farmer can now be informed, with reasonable exactitude, in what respect his animals fail to yield carcasses of the standard required for commanding the top prices per pound in a particular market. He can also be told how these faults may be improved by selection for certain characters, by changing the breed, or the method of feeding, or by some other means. Formerly the farmer had to guess for himself what was wrong when his animals did not grade up to the required standard. This achievement is a result of co-operative work between the scientist and the butcher, who through his practical experience is well aware of the consumers' demand. Numerous workers have employed body and carcass measurements of an arbitrary type to describe body or carcass form. The validity of using such measurements has been proved in recent years. Hirzel (1939), using data on various carcass measurements of all mutton, lamb and beef carcasses exhibited at the Smithfield Fat Stock Shows since 1921, demonstrated that definite relationships existed between certain carcass measurements and carcass quality as judged by the expert butchers at the Shows. From a study of the Champion sheep carcasses of the various breeds he calculated, at different carcass weights, the optimal measurements for some of the more important quality points. Among these were the length of bone (the fore cannon), depth of the 'eye' muscle (*longissimus dorsi*), and the thickness of subcutaneous fat over the 'eye' muscle; both the latter were measured on the cross-section surface of the carcass at the last rib. That certain carcass measurements are correlated with carcass composition has also been proved. In the pig, HANKINS and ELLIS (1934) found a high correlation between the mean back fat thickness and the chemically determined amount of fat in the body. Pálsson (1939, 1940) in widely different breeds of sheep, which were compared at two different ages and at a constant carcass weight at each age, and McMeekan (1940, 1941) in Large White pigs at bacon weight, but at different ages and composition due to treatment differences, both found a high correlation between several external and internal carcass measurements and the total weight of bone, muscle and fat in the carcass. These workers calculated regression equations from which the weight of the major tissues could be calculated from these measurements. Later, WALKER and McMEEKAN (1944) also found high correlations between certain external carcass measurements and the quantitative composition of lamb carcasses at varying weights. Comparison of

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Pálsson's (1939, 1940) results and those obtained by Walker and McMeekan (1944), however, shows that certain measurements may be of great value as indices of carcass composition within a breed though of little or no value between breeds and *vice versa*. Starke (1951) further added weight to Pálsson's results by an extensive study of the relationship between numerous carcass measurements and carcass composition in different breeds of sheep in South Africa.

Some carcass measurements which are of great value as indices of quality such as the depth of the 'eye' muscle are only slightly or not at all correlated with the quantity of any one tissue in the carcass. It should be remembered that carcass quality is affected by shape as well as by composition (see page 522 and MARCQ and STASSE, 1951) A fact, too, which must never be overlooked in the study of carcass composition is that there are three variables to be looked at in a carcass, muscle, fat and bone, and in carcasses of equal weight, if there is a greater proportion of one, there must be less of one or both of the other two remaining; it is the relative proportions of the three tissues which determine the value per pound from the butchers' point of view. CALLOW (1944, 1948) has calculated equations from which the weight of any of the three tissues in beef, mutton and lamb carcasses may be calculated, provided the weight of any one tissue is known and that the carcass contains more than 18 per cent fat.

Mutton and lamb

In no species is the weight of the carcass of such paramount importance as in sheep, whether they be killed for lamb or for mutton. The price per pound is even more dependent on carcass weight than on quality (*Figure 10.56*; Hammond, 1937; Hammond and Murray, 1934). This is so because the consumer often buys whole joints such as the leg, the saddle or the shoulder and requires a certain weight depending on the size of the household. During the last three decades, except for the war years when scarcity of meat resulted in a demand for quantity at the sacrifice of quality, there has been an ever increasing demand for small, compact and not too fat joints of lamb, as compared with the large fat joints of mutton which were in demand half a century ago. This is due to the smaller families of today and increased number of sedentary workers who require less calories than the hard working manual labourer of bygone years. In the large cities of Great Britain there is a still greater demand for the small joints than in the smaller towns and the countryside; in the London market in the prewar years there was great discrimination in price between lamb of the ideal weight and quality and the too heavy or inferior grades due to lack of finish or overfatness (*Figure 10.56*; Hammond, 1937; Hammond and Murray, 1934). To ease the task of the sheep breeder in producing exactly the article wanted in the sensitive London

market, a score card system of grading based on carcass measurements has been developed in countries like Australia, New Zealand and South Africa. This co-operative work by scientists and experienced butchers has been found to be of the greatest value as giving indices of the most desirable conformation and composition of the carcass. However, only at fat stock shows or in carcass competitions involving a limited number of carcasses can the actual measurements be recorded. For large scale grading, photographic standards have been produced so as to ensure that the judges use the same standard in grading, or score card marking, at different places and in different years (*Figure 10.62*). The ideal type of carcass should be of light weight (26–36 lb.), well developed in the hind quarters with blocky legs, short in the bone, fully fleshed and well covered with fat down to the hocks. The crutch should be U-shaped rather than V-shaped (compare No. 1 and No. 3 in *Figure 10.62*). The loin should be full of flesh and well covered with fat, though not excessively so. When the carcass is cut at the last rib both the muscular and fat development is easily measured by calipers or judged visually. In an uncut carcass it is best judged by grasping the loin while the carcass is still warm to feel the fill between the thumb and the second finger. The neck should be short and the fore quarters not too heavy though well filled with meat round the shoulders, with well-sprung ribs having plenty of lean meat on the sides, but not too deep a thorax. Pálsson (1939, 1940) found the fore cannon bone to be the best index both for weight and shape of bone in the carcass (*see* page 495); though the cannon is relatively easy to dissect for exact weighing and measurements the method is too slow except for experimental work. For practical purposes in judging carcass conformation the tibia length or the leg length measured from the bottom of the crutch to the inside edge of the distal end of the tarsals, may be used. A short tibia and a small difference between the leg length and the tibia length is an indication of short bone in general and fullness of meat in the crutch (Pálsson, 1939; Starke, 1951). However, the leg length cannot be accurately measured for comparative purposes unless all carcasses are suspended from a gambrel of constant size. An indirect measurement of the blockiness of a carcass or its fullness of meat is the ratio of weight of carcass : length of tibia, or length of leg. For practical purposes a visual judgment is usually sufficient provided a photographic scale is used. The width of the hind quarters is a good indication of meat development and a high ratio of this measurement over the tibia length, or the leg length, is an excellent indication of compactness of the legs (compare No. 1 and No. 3, *Figure 10.62*). The 'eye' muscle should be deep and come well above the spinous process (No. 1, *Figure 10.62*) as otherwise the muscle will shrink away from it on cooking and give a dry chop which appears to consist largely of bone

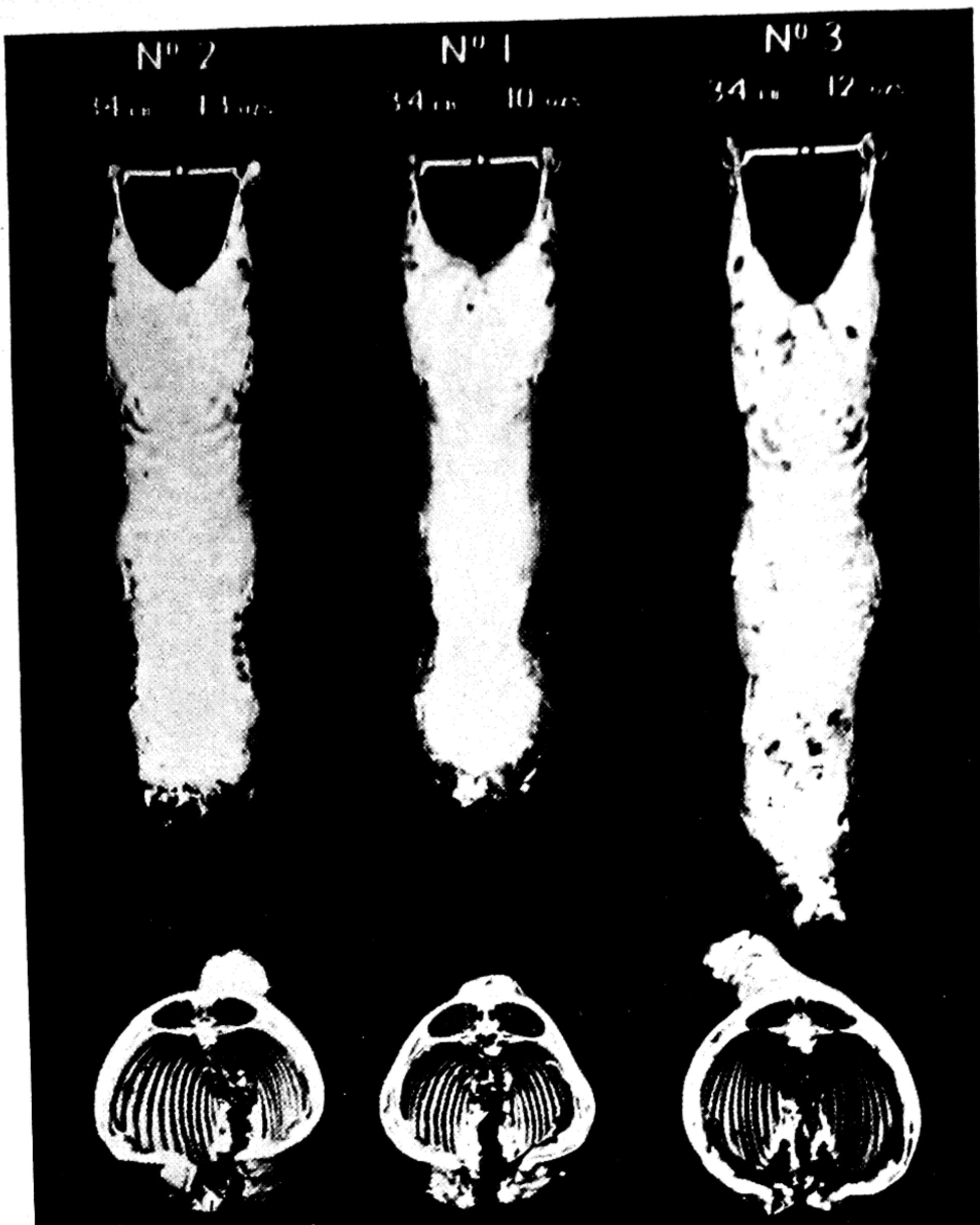


Figure 10.62. The points system of judging lamb carcasses. The number of points awarded for each character enables the exhibitor to know in which respects his carcass falls short of the ideal (No. 1, centre). (a) When the carcass is cut at last rib points are given for the following: *External* (1) Legs, short boned and well filled; (2) Fat covering, sufficient on lower part of legs; (3) Loin, width and fullness. *Internal* (4) Depth of fat over loin, correct proportions; (5) 'Eye' muscle, depth and size; (6) Ribs, light with high proportion of lean; (7) Colour of lean, not too dark; and texture, fine-grained.

	Points No. 2	Points No. 1	Points No. 3
External (1)	24	30	5
	9	10	6
	9	10	5
Internal (4)	12	20	13
	8	15	5
	3	10	2
	5	5	2
	—	—	—
	70	100	38
	—	—	—

(b) When carcass is not cut.

	Points No. 2	Points No. 1	Points No. 3
Legs	26	35	8
Loin	28	35	12
Fat covering	16	30	18
Total	70	100	38
	—	—	—

(Australian Meat Board.)

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(No. 3, *Figure 10.62*). The optimal fat cover over the 'eye' muscle is from 4-5 mm. in lamb carcasses of 26-36 lb. (Hirzel, 1939). *Figure 10.62* illustrates three different types of carcasses and their appraisal (a) where half the marks are awarded for external and the other half for internal characters and (b) where the carcass is not cut at the last rib and the total marks are given for external characters (Hammond, 1952a, b, and Australian Meat Board, 1953). The ideal

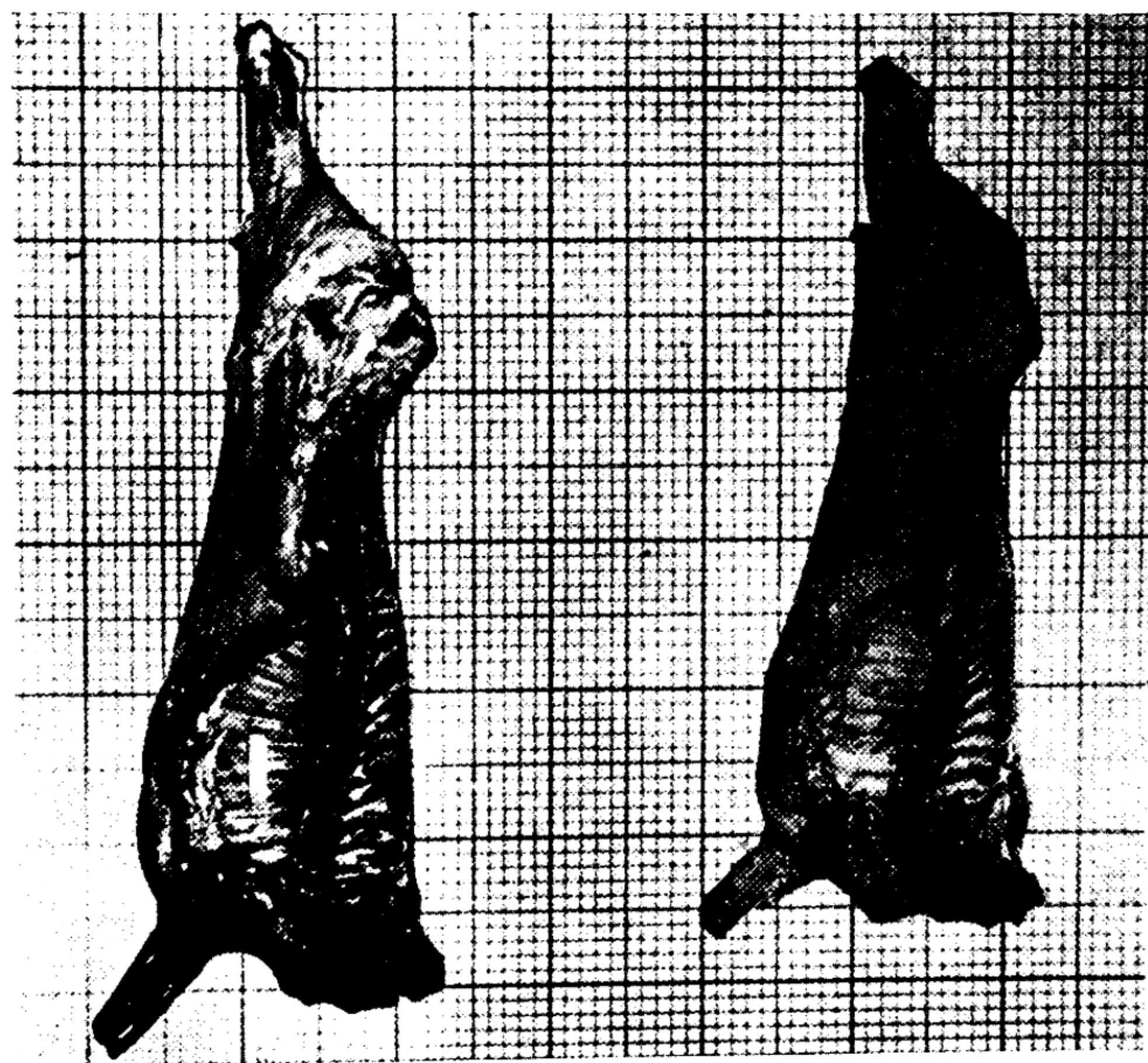


Figure 10.63. Examples of undesirable and desirable beef carcasses.

Left—Undesirable; leg long in proportion to width; neck large; ribs too deep; flat sided. *Right*—Desirable: leg short in proportion to width; neck small; ribs well sprung and not too deep. (From Hammond and Mansfield, 1936, by permission of the Controller of H.M. Stationery Office.)

proportions of bone, muscle and fat in a lamb carcass are not yet exactly known. However, the work of CLARKE and McMEEKAN (1950) and CLARKE *et al* (1952) has done much to elucidate this point. They found in a random sample of New Zealand 'Prime Down cross' and 'Prime Canterbury' lamb carcasses of under 36 lb., which are considered to be the highest quality lamb in the world, that in the former bone accounted for some 10.9%, muscle 50.5% and fat 33.6% of the carcass weight, while corresponding figures for the latter were 11.7%, 52.5% and 32.7%. Inedible tissue, tendons and spinal cord amounted to 3.5% and 2.4% in the two lots respectively. This type of carcass excels most of all other lamb carcasses at light weights due to the lightness of bone and good finish

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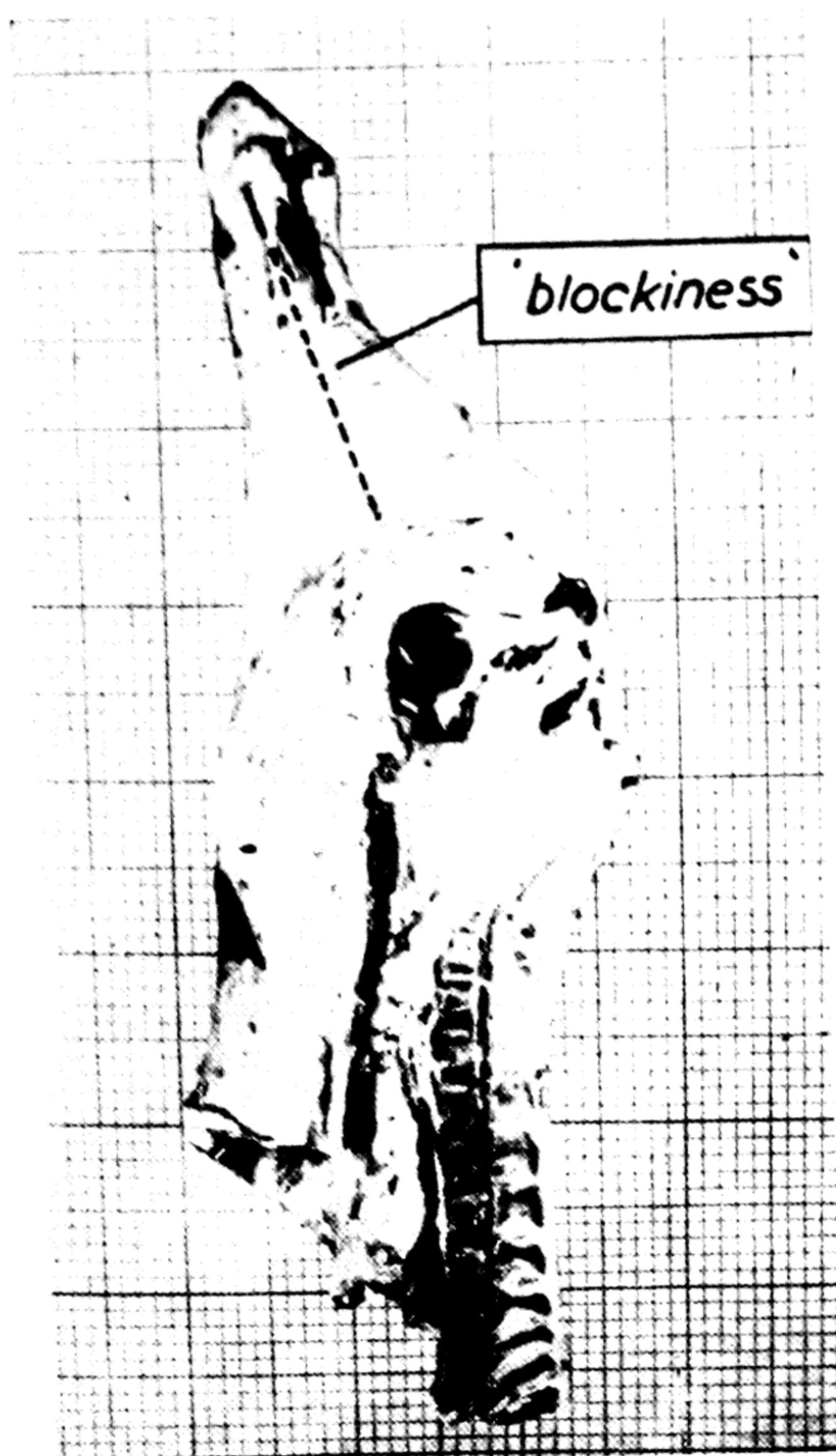


Figure 10.64. The New Zealand points system of judging beef carcasses.

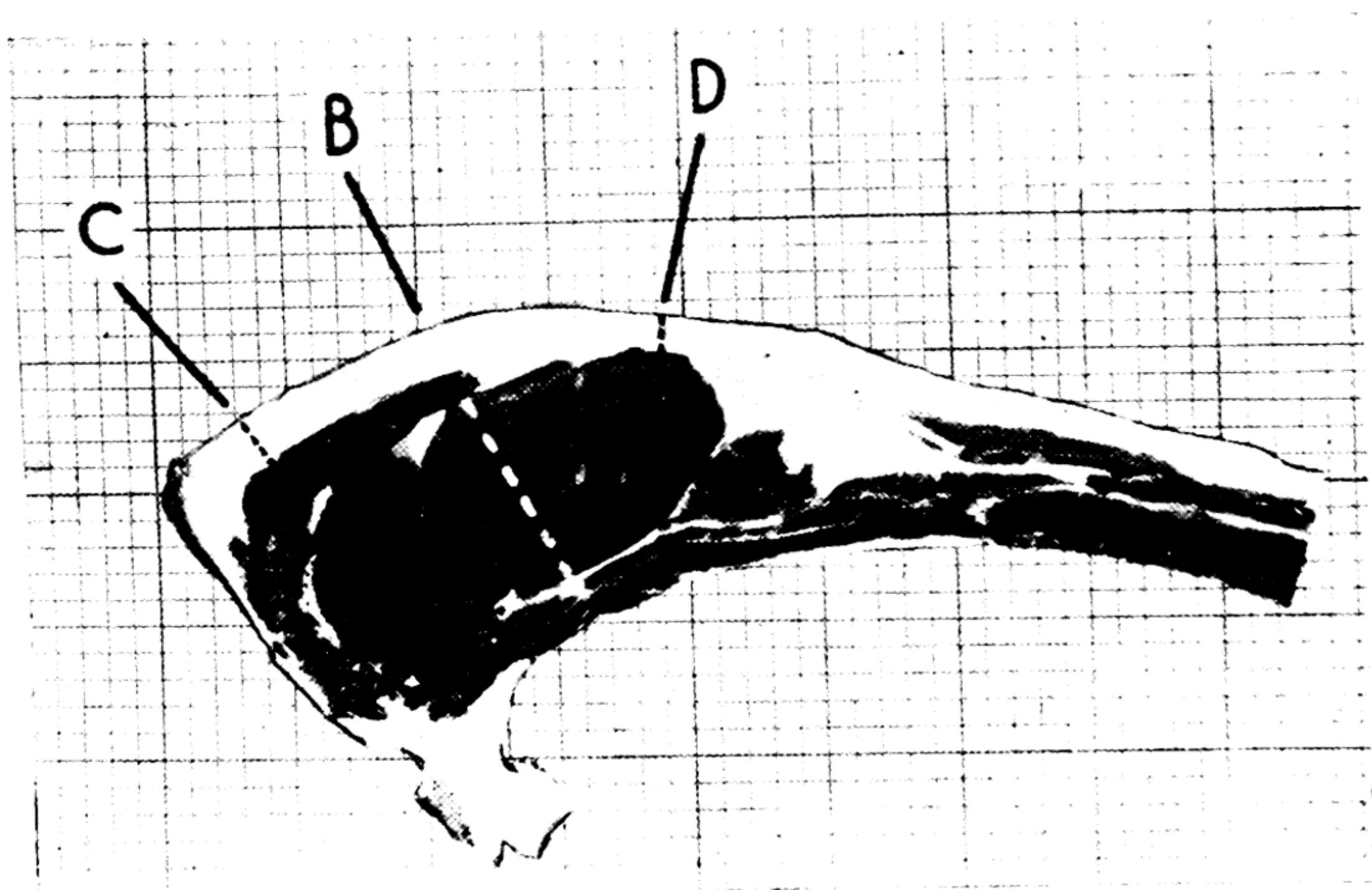
By Measurements Full Points

1. Fullness of meat ('eye' muscle depth) B . . .	20
2. Fat cover (depth over 'eye' muscle) C & D . . .	15
3. Blockiness (Leg length) T . . .	20
4. Balance of Carcass (Fore-end-Hind-end weights) . . .	10
5. Weight suitability . . .	5
	— 70

By Eye Judgment

6. Rib cover and evenness of fat distribution . . .	15
7. Colour and texture of muscle	5
8. Colour and texture of fat	5
9. Marbling of muscle	5
	— 30
	—
Total	100
	—

(From Kneebone *et al*, 1950, by courtesy of *N.Z. J. Sci. Tech.*)



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but is inclined to become overfat at heavy weights (Pálsson, 1939, 1940; Walker and McMeekan, 1944; Clarke and McMeekan, 1950). The work of Pálsson and Vergés (1952) (see pages 478-496) shows that for the production of top quality lamb in a short season a high plane of nutrition throughout is essential so that plenty of flesh is produced and sufficient subcutaneous fat cover is obtained before the bones reach great length. A good quality carcass can also be produced by a low plane of feeding first followed by a high plane but this method is essentially less economical and requires a longer season. A high plane feeding first followed by a low plane results in the poorest quality of lamb, heavy in the bone and too lean.

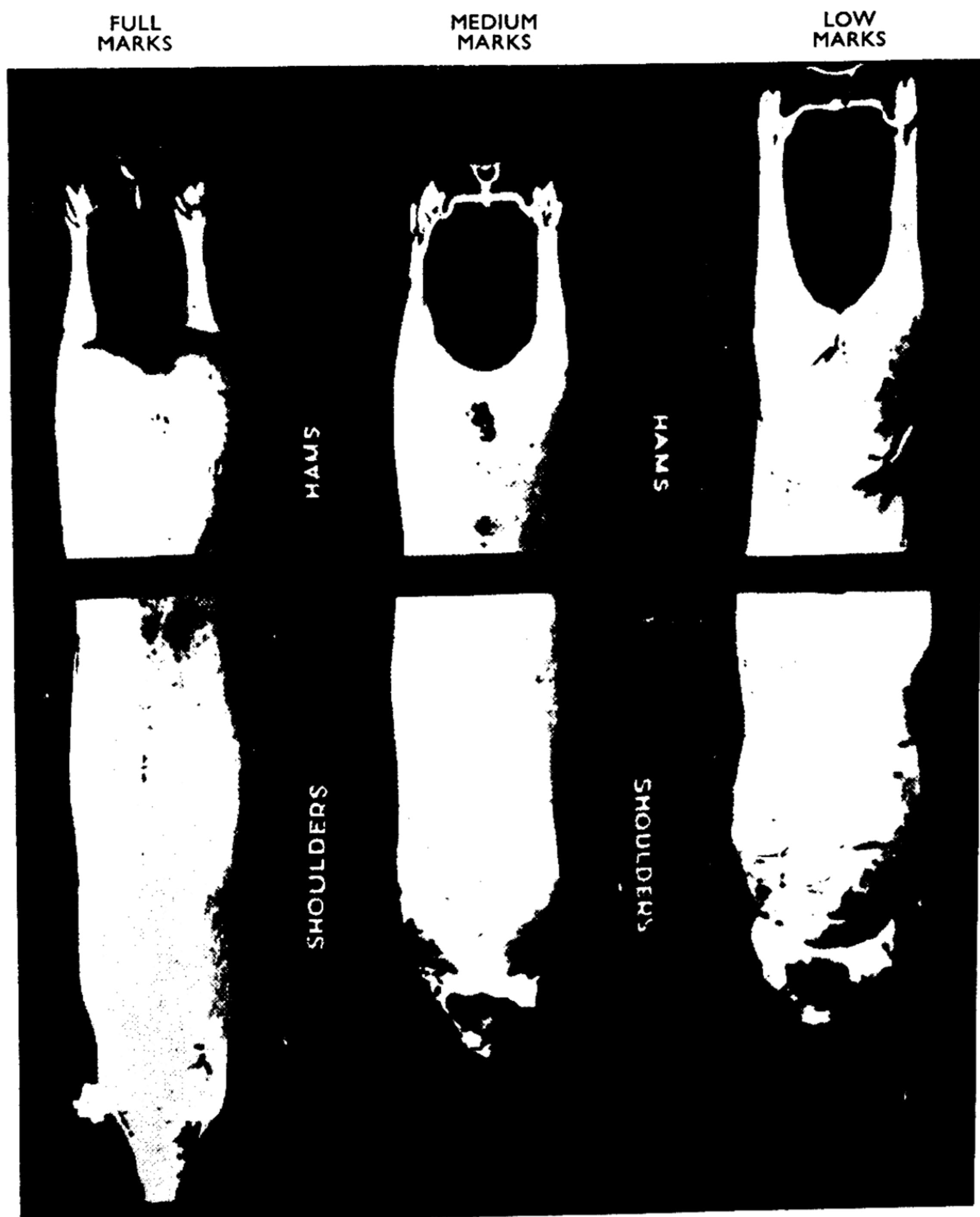


Figure 10.65. Photographic standards used in judging hams and shoulders. (From Davidson *et al*, 1936-37, by courtesy of *The Pig Breeders' Annual*.)

Beef

The modern requirements for beef are for a small sized carcass of 550–650 lb. which has been quickly grown; it should have well developed back and hind quarters and relatively light shins, neck and brisket (*Figure 10.63*; Hammond, 1952a). For a good type of carcass early maturity and slaughtering at a young age are essential, as otherwise the fore quarters become too deep and heavy in proportion to the loin and rump (compare No. 14 with No. 13, *Figure 10.16*). A deep 'eye' muscle with a suitable fat covering (24 mm. in a 600 lb. carcass) and plenty of marbling fat in the muscle is a most desirable character (*Figure 10.64*). A scale of points for judging beef for the London market has been drawn up in New Zealand by KNEEBONE *et al* (1950), and for Belgium by Marcq and Stasse (1951). The usual practice of cutting beef carcasses between the tenth and the eleventh ribs exposes the development of the 'eye' muscle and the fat covering over it, so awarding points is easier in beef than in lamb. *Figure 10.64* illustrates the measurements taken and the scale of points for New Zealand beef (for details see Kneebone *et al*, 1950). The most desirable composition of the beef carcass is not yet known with a high enough degree of accuracy; the quality of both beef and lamb is more affected by the distribution of the fat than by its actual amount. However, Callow (1944) found that from the palatability point of view a muscle : fat ratio of about 1.5 : 1 was the most desirable proportion of these tissues, the palatability increasing up to about 40 per cent of fat in the boneless beef and declining with greater fatness. The plane of nutrition affects beef carcass quality in much the same way as lamb (pages 478–496). However, as beef animals have to be kept over at least one and often over two winters a high plane feeding throughout is not necessarily the most economic method of rearing (BROOKS and VINCENT, 1950; see Chapter 9, p. 403).

Pork and Bacon

As for lamb and beef, so points scales for judging pork and bacon have been evolved by DAVIDSON *et al* (1936–37), by the New Zealand Judging Standards Committee (1952), by the National Pig Breeders' Association (1948), and for bacon by Clausen (1938), RIJSSENBECK (1937) and OLOFSSON (1951). McMeekan (1940, 1941) has described how the measurements can best be recorded and which are of greatest value as indices of carcass quality and composition. These different scales are chiefly a result of different circumstances under which the carcasses are judged, whether fresh, frozen or cured, whole, split along the back or cut across at the last rib. For the London Market a fresh pork carcass should be short legged, with a long body, well developed hams and relatively light in the fore quarters, with a deep round 'eye' muscle and not too fat. Maximum points are given for

a carcass of 70-74 lb. with an 'eye' muscle depth of 46 mm. and fat covering of 10 mm. combined with ideal hams and light shoulders (*Figure 10.65*). The enormous differences which may exist in the muscle and fat development in the loin region of porker carcasses of equal weight is illustrated in *Figure 10.66*. For maximum points according to New Zealand Standards (1952) a bacon carcass should weigh 146-150 lb. and have a body length of 82 mm. from the

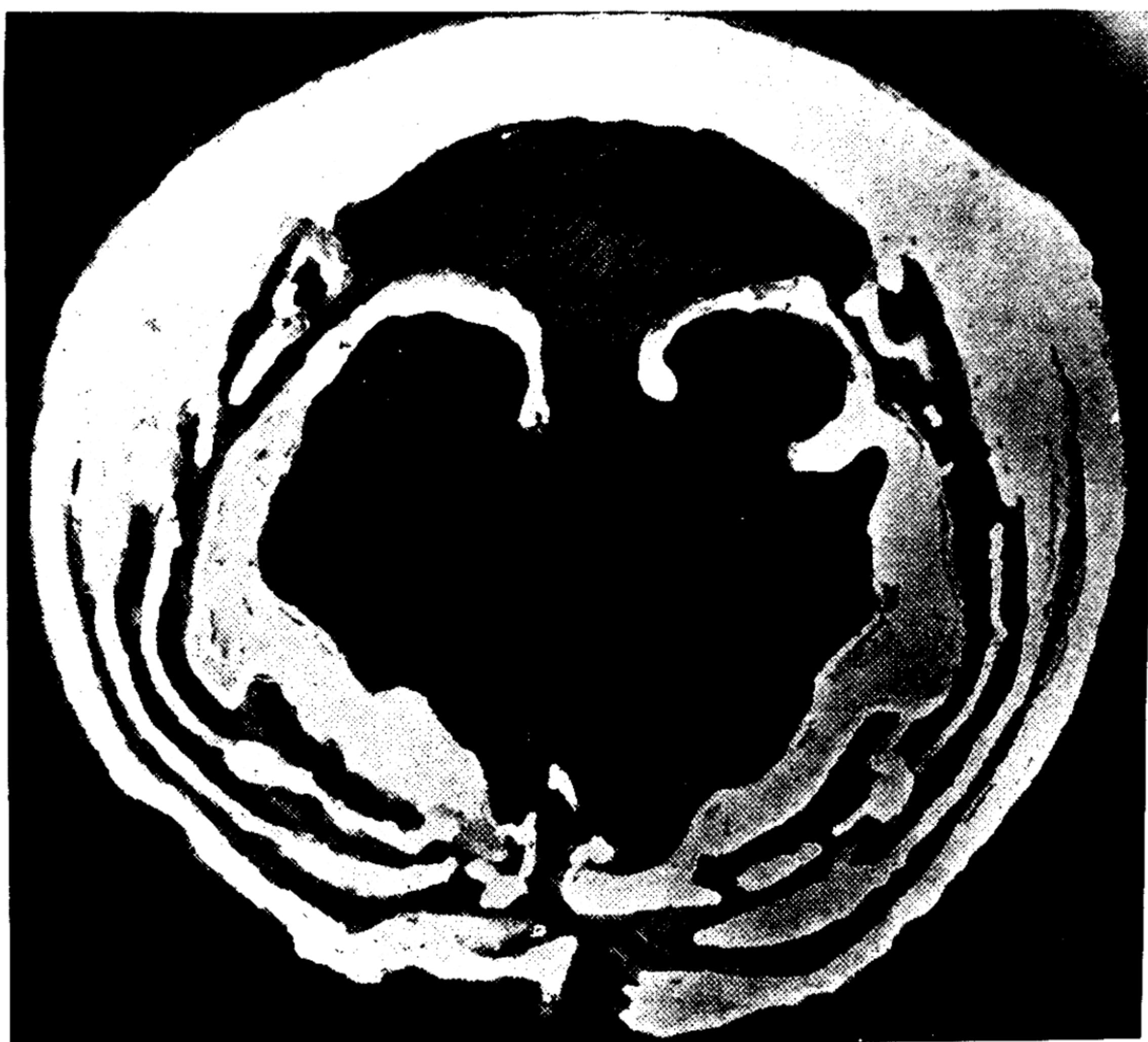


Figure 10.66. Sections of porker carcasses of same weight. *Above*—Poor muscle and excessive fat. *Opposite page*—Excellent development of muscle and sufficient fat. (From New Zealand Judging Standards Committee, 1952, by courtesy of *N.Z. Dept. Agric. Bull.*)

symphysis pubis to the anterior edge of the first rib at the sternum. It should have well developed hams and a shallow thorax, not exceeding 40 per cent of the body length. The back fat thickness at the shoulders and at the loins should be 23 and 15 mm. respectively. The ideal 'eye' muscle thickness is 56 mm. and the back fat covering over it at the last rib is 21 mm. (Hammond, 1952b). The most common faults in a bacon carcass are too poor muscular development and excessive fatness, often indicated by a short body, heavy fore quarters and poorly developed hams. However, only cutting of the carcass

at the last rib can show up relative development of muscle and fat with any degree of accuracy. Softness of fat in pork and bacon is often a serious fault (*see* page 527); this is best judged by the touch of the thumb. The plane of nutrition greatly affects the carcass quality of bacon pigs (pages 503-507) but in a way quite contrary to that of lambs (McMeekan, 1940, 1941; Pálsson and Vergés, 1952). The best bacon carcass is obtained by high plane feeding during the



Figure 10.66 (continued).

early stages followed by a low plane. This encourages muscular development but retards fat deposition, whereas a low plane feeding followed by a high plane has the opposite effect, resulting in an excessively fat carcass with poorly developed muscle (*see* pages 503-507 and *Figure 10.50*).

Although carcass measurements are very useful for all practical experiments involving changes in size and body proportions, and can be used for judging standards, they are, however, not sufficiently accurate for highly scientific growth studies. For such cases dissection of sample joints as described by Pálsson (1939, 1940), McMeekan (1940, 1941) and Starke (1951), or complete dissection of the whole body is necessary to acquire exact information about the growth of the different tissues in the different parts of the body. Chemical analysis

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in connection with dissection is useful in many cases. To measure changes in live weight and even in carcass weight is of relatively little value indeed in scientific growth studies as such changes do not elucidate the differential growth of the various tissues and parts of the body.

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CHAPTER 11

WOOL GROWTH

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THE HIGHLY evolved wool sheep is an outstanding example of artificial selection. Its fleece, unlike the pelage of its primitive ancestors which is shed periodically, grows continuously, and would become an intolerable burden if left unshorn. Its integument is densely populated with follicles that produce wool at a rate which is grossly in excess of the animal's needs for heat conservation and which imposes nutritional demands that are in many ways unique.

This brief chapter endeavours to essay broadly our present knowledge of the biology of the sheep's integument, and of the physiological and nutritional factors which influence wool growth, rather than to discuss in detail any one particular field of this not especially well cultivated estate of knowledge. To render this possible in the small space allotted, a reluctant decision was made to exclude a bibliography, as acknowledgments, if they were to be adequate, would extend many times the length of this chapter. The subjects mentioned here will be discussed in greater detail in a review that is being prepared by the author for *Nutrition Abstracts and Reviews*, in which a full bibliography of the subject will appear.

THE PHYLOGENY OF HAIR

Attempts that have been made to establish phylogenetic relationships between mammalian hair and non-mammalian epidermal structures, from morphological evidence alone, have resulted in a wide diversity of opinion. An hypothesis which traces hair back to the placoidal scales of elasmobranch fishes and thence to the teeth of the amniotes, though appealing, is weakened by lack of evidence that mammals are derived from any form with placoidal scales. A suggestion—that sense organs in the skin of fishes and of aquatic amphibia were the precursors of hair, because the early stages in the development of both structures are remarkably alike, has been opposed as there is little or no evidence of transitional stages. An opinion that hairs correspond to the scale-borne tactile spots of reptiles to which in their

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early developmental stages they bear striking resemblance, and an hypothesis, arising from a study of the coat of the monotreme, *Ornithorhynchus*, which added further support to the suggestion that the hair and the axial shaft of the feather are both derived from the scales of a common reptilian ancestor, share the embryological objection that hair-follicles begin essentially as modifications of the epidermis whereas scales and feathers are initiated in the mesenchyme. And, in despair of reaching agreement, there is the conclusion that hair is a mammalian entity *de novo*, a morphological structure *sui generis*, for which there is no known antecedent in the lower forms.

All of the hypotheses mentioned above assume a phylogenetic individuality for scales, cutaneous sense organs, hairs, feathers, etc., which need not be insisted upon. Each of these structures is a product, not of a single specific entity in the germ-plasm, but of a complex set of genetical factors that concern the pelage as a whole, any of which may become modified in the course of phylogenetic history. If then the homologies of hair with scales, cutaneous sensory organs etc. be considered relative rather than absolute, most of the theories which aim to explain their evolution may be reconciled.

Structures similar to hair follicles have been described in the integument of the fossil remains of an aquatic reptile, *Ramphorhynchus*, but apart from anatomical considerations, the physiological process of keratinization common to the production of all of these structures was certainly already established in the reptilian scales.

HAIR TYPES

Apart from the tactile vibrissae, large hairs which are pre-eminently sensory organs that arise from follicles embedded in erectile tissue and surrounded by a rich network of nerve fibres, the hairs of the protective coats of mammals are classified into two main groups; the coarser guard hairs, many of which also have nerve fibres at the base, and the finer hairs of the undercoat. The guard hairs may be subdivided further into: the *Spines*, which comprise the large, defensive hairs and quills; the *Bristles*, the firm but less coarse hairs, variously called Leithaar, Transitional hairs, Protective hairs, Primary hairs, etc.; and the *Awns*, the Grannenhaar, hairs which are strong at the tip but fine at the base. The finer, softer hairs of the undercoat may be subdivided into *Fur*, which is comprised of relatively short, straight, soft, fine fibres; *Wool*, which is comprised of relatively long, non-medullated, curled or crimped, fine fibres; and *Lanugo* or *Vellus* hairs, that are respectively the pre natal and post natal forms of the finest and shortest hairs.

The fleece of the primitive sheep is homologous with the hair-coat of wild animals: it has an outercoat of bristles and awns which are

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generally referred to as kemp fibres and heterotype fibres respectively, and an undercoat of wool. Each of these classes of fibres is recognizable in the birth-coat of domesticated breeds, even in the fleece of the Merino lamb. The medullated kemp fibres are shed soon after birth, and, in most breeds, do not reappear; the heterotype fibres either persist, as they do in the outercoat of the British mountain breeds, or may, in other breeds, become modified to a greater or less degree to approximate to true wool fibres, as they do in the adult Merino fleece.

THE ONTOGENY OF WOOL FOLLICLES AND ITS IMPLICATIONS

The follicles of the mammalian hair-coat tend to develop as recognizably discrete groups, frequently comprised of three follicles so disposed as to suggest the scale-form of non-mammalian ancestors.

Early histological studies of the skin of the *Ovinae*, revealed two types of follicles—those of the *Leithaar*, which are differentiated first and which produce the strong hairs of the outercoat, and those of the *Gruppenhaar* which develop later in clusters about the original groups and which produce the finer fibres of the undercoat. More recent embryological investigations of the ontogeny of skin structures in the Merino foetus have indicated a protophase, extending from 65–85 days of intra-uterine life, during which period the primary follicles are laid down, usually in groups of three; and a neophase, extending from about 85 days to full term and for a considerable period after, during which secondary follicles develop in more or less loose patterns about the basic primary trios. The primary follicles have a full complement of accessory structures—a simple apocrine sudoriferous gland, a bifurcated involuntary muscle, the *arrector pili*, and a large bi-lobular or multi-lobar acinous sebaceous gland: the only accessory structure associated with secondary follicles is an occasional sebaceous gland which in these is small and relatively simple, generally uni-lobar. The follicular group aggregation in the skin of the Merino is thus comprised essentially of three primary follicles and a variable number of secondary follicles, the final relationship between the two categories depending fundamentally on hereditary factors, though it is subject to modification during growth and development.

There is a marked antero-posterior gradient in the initiation of the follicles in the integument of the Merino foetus: crowding of epidermal cells into the foci which become the *anlagen* of the primary follicles is discernible about the 50th day of intra-uterine life, first of all in the region of the poll, and from there during the ensuing 10 days differentiation of these primordia spreads as a wave over the whole surface of the body. Initiation of secondary follicles begins

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about the 80th day and proceeds similarly. At this stage there is little indication of the marked dorso-ventral gradient in the follicular-density distribution which later in the course of development becomes so obvious, but at birth this is already clear.

Experimental observations, not so complete as those that have been made in the Merino, indicate that the development of the follicles in other breeds follows a similar course.

Apparently the first follicles that are formed, retain most avidly the primitive tendency to produce medullated fibres. Studies of the distribution of kemp fibres in Romney Marsh fleeces imply that the population density of the follicles that produce them decreases in an orderly antero-posterior gradient over the wool-bearing surface. The primary follicles are initiated in a similar gradient and the fibres from them are certainly more subject to medullation; the relatively few secondary follicles that are thought to produce medullated fibres are those that differentiate earliest in the ectal region of each follicle group.

The composition of the mature follicle-group varies widely from breed to breed: in the fully developed integument of the pure Merino, eighty or more secondary follicles are grouped around each trio of primary follicles, whereas in the integuments of Border-Leicester and Lincoln sheep the follicle-group that surrounds a trio of primaries rarely has in it more than twenty secondary follicles, though in the mature animal the area of skin covered by a follicle-group is closely similar in all three breeds.

Studies of the ontogeny of the skin structures in the Merino indicate that primary follicles cease to be laid down in the integument of the sheep after the end of the protophase of follicle induction which finishes about the 90th day of foetal life, and there is little doubt that any contribution to the total fibre population subsequent to the protophase is made by the further differentiation of secondary follicles. If then the population of primary follicles in the integument remains practically constant after the lamb is born, the ratio of the number of secondary follicles to the number of primary follicles, S/P , which may be estimated by microscopic examination of suitably prepared skin sections, should provide a quantitative means of assessing changes that occur in the fibre population.

Periodic estimation of the S/P ratios in the integument of the Merino indicates that the differentiation of secondary follicles, which begins with the neophase about the 80th day of foetal life, proceeds comparatively rapidly during the first 100 days or so after birth, and thereafter more slowly towards an asymptote which is closely approached when the sheep is about twenty months old. If the growth of the lamb is retarded by suboptimal nutrition, the rate of development of new follicles is diminished and the animal never attains the full

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complement prescribed by its genetical constitution (*Figure 11.1*). Reduction of the final follicle population induced in this way is distinct from change in the relative growth of the integument; the latter is an independent variable and is also influenced manifestly by the nutritional environment.

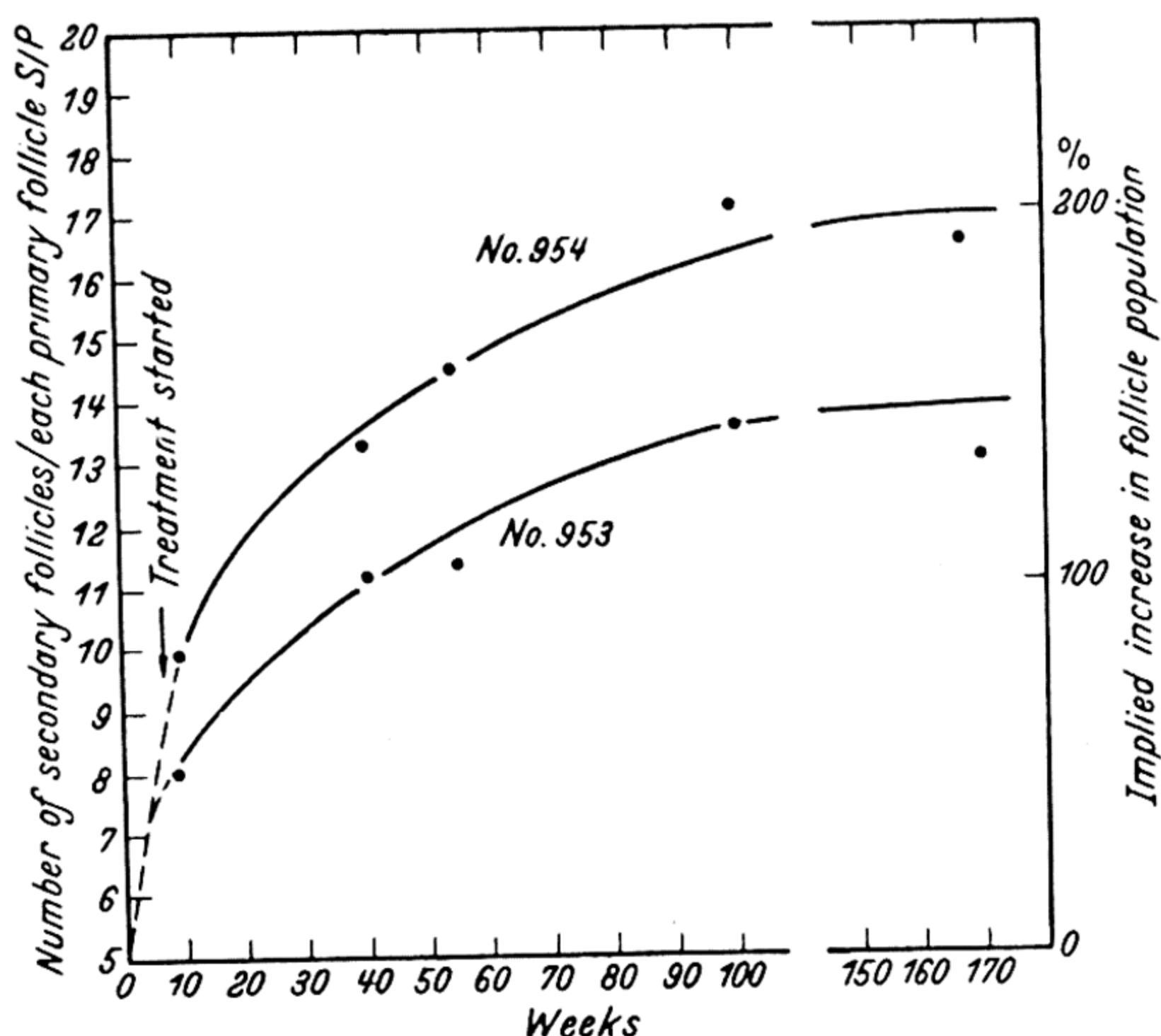


Figure 11.1. The trends of the induction of new follicles in the integument of the strong-wooled Merino as indicated by the S/P ratios, suggest that secondary follicles continue to be formed for about two years after birth. The twin lambs on which these observations were made are discussed in the text; they were of a strain in which the follicular group at birth contains between 12 and 15 secondary follicles to each trio of primary follicles *i.e.* an S/P ratio between 4 and 5. The scale to indicate the implied increase in total population is based on the assumption that, when each animal was born, the S/P ratio in the particular skin area studied was 5. The retarding influence and the final effect of malnutrition are indicated by the performance of No. 953. (Compiled from estimations made by H. B. Carter, in experiments of Marston, Peirce and Carter, 1940-43.)

Little is known of the nature of the physiological forces responsible for the induction of follicles in the integument. There is strong evidence which suggests that the dermis of the Merino retains some capacity to initiate follicles until the animal is about two years old, though its power to provide these follicles with a full complement of accessory structures is restricted to a brief period of 40-50 days of

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foetal life—all follicles produced subsequent to this period are secondary follicles, which, by definition, are devoid of both sudoriferous glands and *arrector pili* muscles, and frequently, of sebaceous glands.

Stimulatory effects on the pelage of laboratory animals produced by adrenalectomy or by dosing with thyroxine are due essentially to the awakening of resting hair-follicles into functional activity, not to the induction of new ones. The removal of the thyroids from young Merino lambs leads to a very considerable reduction of wool growth which, in greater part but probably not wholly, is due to metabolic changes that lead to a diminished food consumption.

THE HISTOGENESIS OF THE WOOL FOLLICLES

The epithelial bud of the developing follicle, which begins as a crowding of cells in the deep layers of the epidermis, elongates into the dermis, and during progression downwards the growing end enlarges into a bulb which becomes invaginated by the protrusion of a connective tissue papilla into its base. The peripheral layers of the main stem of this epithelial ingrowth shrink away and differentiate to form the outer root-sheath; the core retains its continuity with the malpighian layer of the epidermis, and differentiates into the shaft of the fibre and the Henle and Huxley layers of the inner root-sheath. When the follicle matures and becomes functional, the cells that are destined to become the keratinized cuticle and cortex of the fibre and the semi-keratinized, vitreous layers of the inner root-sheath, proliferate from a matrix which is contiguous with the papilla.

During the development of the primary follicles in the integument of the sheep, the matrix cells around the top of the papilla are pushed by connective tissue much further into the bulb, from which site they multiply and form the poorly keratinized medulla characteristic of kemp fibres. When the primary follicle has shed its initial fibre-growth, as it does, irrespective of the breed, within the first few months of the lamb's extra-uterine life, the matrix of the bulb may become modified and subsequently produce a non-medullated fibre. After shedding the primary fibres of the birth-coat, the regenerated follicles in the integuments of some breeds of sheep retain their propensity both for medullation and for periodic shedding. This primitive tendency to form a medulla is delicately poised in these follicles, however, as after each shedding the newly grown fibre may or may not be medullated. In the Merino, the fibres produced from the primary follicles after the lamb's halo hair-coat has been cast, grow, like those from the secondary follicles, as a solid, continuous filament. In some of the Australian strong-woollen Merino strains, these fibres, as a class, are considerably stronger and longer than those produced by the secondary follicles, and, in extreme instances the appearance they

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impart to the fleece of the mature animal is reminiscent of the outer-coat of the primitive sheep, though this similarity is never so striking as that exhibited by the Romney Marsh.

THE HISTOLOGY OF THE WOOL FOLLICLES AND THE BIOCHEMISTRY OF FIBRE GROWTH

As the cells of the matrix proliferate and mature in the functioning follicle, their expanding protoplasm sets up a pressure within the bulb which forces them to present a minimum surface and fill with no interstices the restricted space they occupy ; the mass of cells assumes

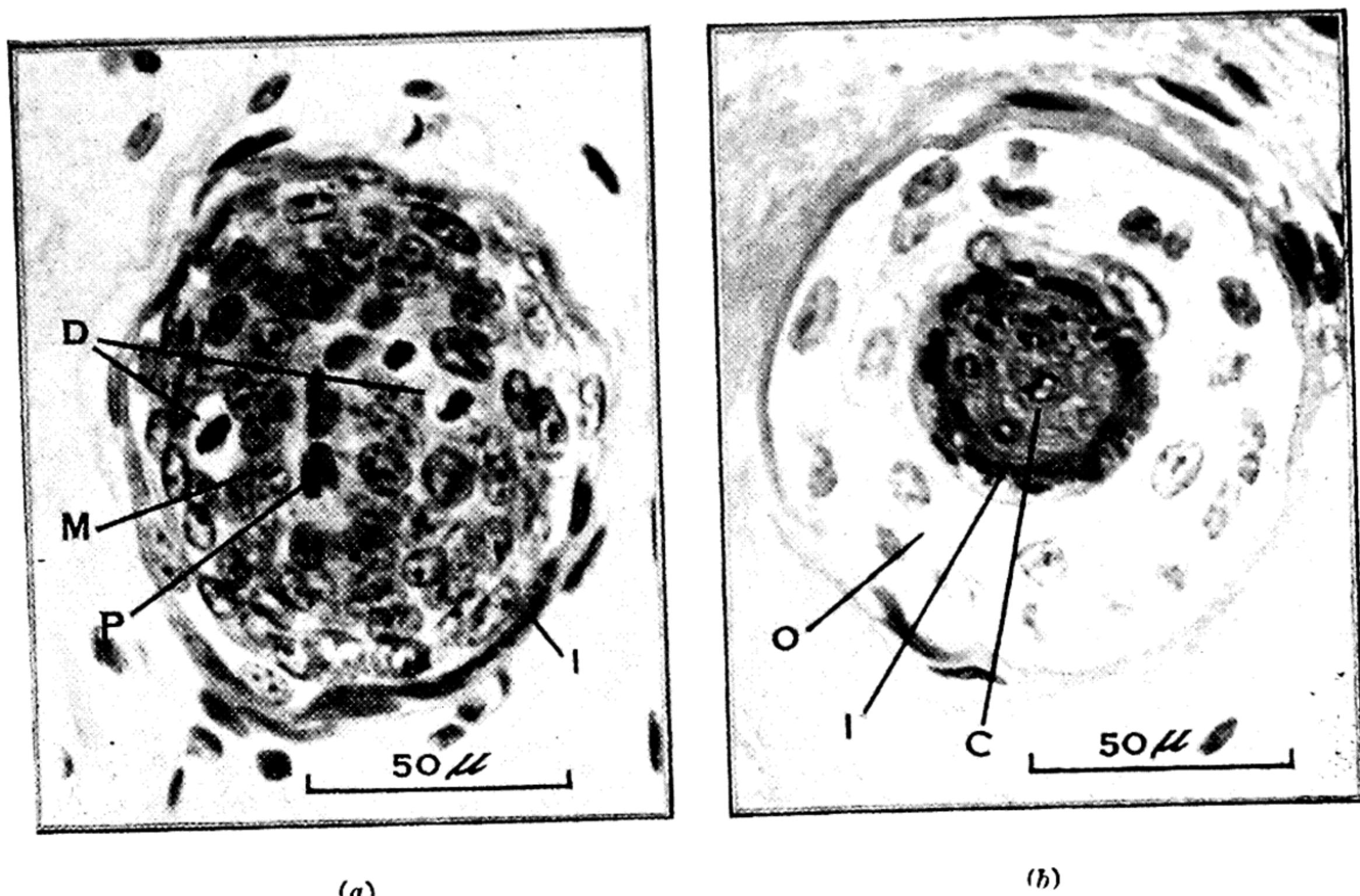


Figure 11.2. (a) Transverse section through the widest part of the bulb showing actively dividing follicular cells, D, in the region of the matrix, M, and the relationship of the latter to the papilla, P. At this level the cells of the inner root-sheath, I, are in the early pre-keratin stage and contain deposits of trichohyaline. (b) Transverse section through the neck of the bulb of the same follicle as (a). Note the closely packed extruded mass of cortical cells, in some of which the elongated nuclei have been sectioned. At this level the cells of the inner root-sheath, I, have not completely lost the trichohyaline deposits. Note also the wide band of outer root-sheath cells, the ratio of the diameters of the bulb and its neck shows clearly the extent of compression to which the cells are subjected during their extrusion. (H.R.M.)

a foam-like structure in which each cell becomes faceted and approximates the shape of a minimum tetrakaidecahedron. The dividing cells below push this plastic mass towards the constriction at the neck of the follicle where the individual cells become compressed to a relatively small fraction of their original cross-section, and so all but those at the periphery become greatly elongated into

the spindle-shaped cells which later, when keratinized, comprise the cortex* of the wool fibre. The peripheral layers keratinize early into the flattened cells of the fibre-cuticle and the inner root-sheath.

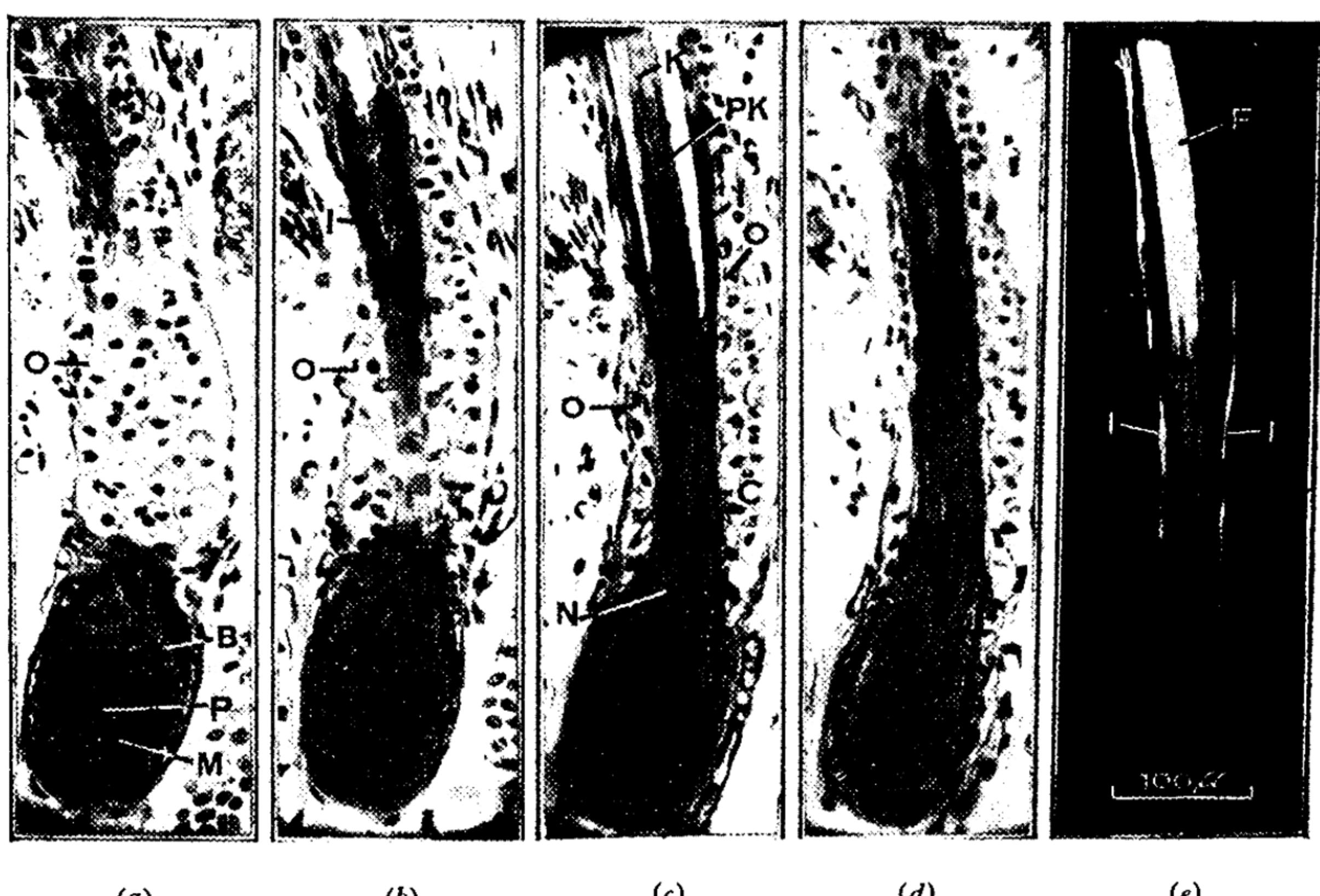


Figure 11.3. (a)–(d) The main histological components of the wool follicle are illustrated in these serial sections cut longitudinally through the lower portion of a primary follicle from the integument of a Merino sheep. Note the invaginated papilla, P; the matrix cells, M; the comparative massiveness of the bulb, B, in relationship to its constricted neck, N, through which the cortical cells are extruded. The strongly reducing, pre-keratin region of the fibre shaft, PK, changes quite abruptly to the fully keratinized fibre, K, which has little affinity for the basic dyes. The outer root-sheath, O, is intact; the inner root-sheath, I, is normally closely contiguous with the fibre to levels well above those shown in these sections; its shrinkage away from the shaft at this low level is a fixation artefact. (e) Shows the section (c) in polarized light. Note that the birefringence, which is quite marked in the fibre shaft just above the neck of the bulb, reaches a maximum in the pre-keratin region and remains unchanged when the fibre, F, is fully keratinized. The inner root-sheath, I, which is first to keratinize becomes birefringent about the level of the summit of the bulb. (H.R.M.)

Keratinization of the cells of the inner root-sheath, and of the medulla, if the follicle produces one, takes a different course from that of the cells which become cortex and cuticle of the fibre. Trichohyaline forms as discrete, highly refractile, acidophilic globules within all of the former cells during the earliest transitional stage of their

*The fully keratinized part of the hair-fibre which ensheathes the core of poorly keratinized medullary cells is called, appropriately, the cortex—literally, the bark. By usage, the word cortex has been retained to signify the fully keratinized portion of the fibres of the mammalian hair-coat irrespective of whether a medulla persists. Thus the non-medullated wool fibre consists essentially of two parts, the solid thread of cortex and its cuticular sheath.

keratinization, but it never becomes evident in the cortical cells nor in the cells of the fibre-cuticle, although these latter are contiguous with the cuticular cells of the inner root-sheath for a period during their passage upwards. Apart from this difference, transformation to keratin proceeds similarly in all of the epithelial cells arising from the matrix. In those cells which differentiate into the concentric layers that comprise the inner root-sheath, trichohyaline usually makes only a transitory appearance though some may persist. Histochemical evidence indicates that the contents of these cells subsequently pass through a series of changes very similar to, if not identical with, those which take place during the keratinization of the cells that later form the fibre itself.

The rates at which these transformations proceed in the various layers differ markedly. The outermost cells—those of Henle's layer—are the first to keratinize. In these, the process begins early while the cells are passing the widest portion of the base of the follicle; and it progresses rapidly, for these cells are completely keratinized before they reach the summit of the bulb. The flattened cells that form the cuticle of the fibre are next to keratinize. In the cells which comprise the Huxley and the cuticular layers of the inner root-sheath, the transformation proceeds more slowly, at a rate similar to that of the cortical cells of the fibre, and so for a period both of these layers remain incompletely keratinized while confined between two concentric bands of fully keratinized cells. In consequence of this early keratinization of the fibre-cuticle and of the Henle layer, all substances passing into or out of the cortical region during the final stages of its keratinization must traverse, by diffusion, two intervening concentric layers of keratinized cells. The cells of the inner root-sheath, when keratinized, become converted to soft-keratin, which is characteristic of the cornified epidermal cells that originate in the malpighian layer of the epidermis with which the inner root-sheath is continuous. They desquamate on nearing the skin surface and are pushed out of the orifice of the follicle by the growing fibre.

During its passage upwards, the cortical cell undergoes a series of changes that are typical of the formation of hard-keratin. Its protoplasm granulates and, in part, aggregates into micro-fibrillae which become aligned, closely parallel to the fibre shaft, by the shearing stresses set up when the cell is elongated during its extrusion through the neck of the bulb. While in this state these tono-fibrils coalesce into bundles; later the nucleus disintegrates, the nuclear remnants disappear, and the mass of elongated cortical cells is transformed into an apparently homogeneous filament of keratin.

The foam-like mass of cells in the lower part of the bulb is isotropic—it has little if any tendency to birefringence in polarized light, and no evidence of the semi-crystalline molecular state that is characteristic

of the keratinized fibre is revealed by the x-ray diffraction pattern of this zone. On approaching the summit of the bulb, at the level where the cells begin to elongate, the cell-mass becomes birefringent, and, as it passes upwards towards the narrow neck of the bulb, the intensity of this indication of preferred molecular orientation within the cell-substance increases rapidly to a maximum which thereafter remains unaltered in the fibre shaft. This relatively sudden appearance of birefringence in the uppermost region of the bulb is coincident with the formation of fibrillae within the protoplasm of the cells, and it increases in the elongating cells as the shearing stresses progressively orientate these tono-fibrils parallel to the fibre axis. The cell-mass begins to dehydrate at this stage and the x-ray diffraction pattern becomes that of α -keratin which is characteristic of the completely keratinized fibre.

For a period during its progress upwards, the cell-mass develops a very strongly negative oxidation-reduction potential and the presence of free thiol groups ($-SH$) may be demonstrated in it by treatment with alkaline nitro-prusside or by other means. While in this state the cell contents remain plastic—they may be disorientated by heat, and they may readily be dispersed by concentrated urea solutions. Keratinization is completed by the oxidative closure of the thiol groups in adjacent polypeptide chains. The mass, thus becomes bonded with the co-valent dithiol linkages ($-S-S-$) that play a major part in maintaining the specific molecular configuration of keratin. This final stage of keratinization is effected while the plastic mass of cells is still under tension. When freed from fully keratinized wool fibres by retting, the cortical cells retain their elongated form, but if they are treated with reagents that rupture the dithiol linkages, they contract and assume proportions reminiscent of the shape they originally had within the bulb of the follicle. The oxidative closure of the thiol groups, which converts the reduced pre-keratin to keratin, is catalysed either directly by copper-ions or by copper-containing enzymes.

In the latter stages of keratinization the refractive indices of the morphologically discrete structures within the cells become so closely similar as to lead to the virtual disappearance of visible differences between the fibrils and other components: the cell contents and later the cells themselves lose their identity and the wool cortex fuses into an optically homogeneous filament. This apparent homogeneity is misleading, however, for while there is little doubt that the cortical mass is composed of keratin, there is good evidence that this keratin occurs in at least two distinct physical states within the wool cortex: a phase comprised of the persistent fibrillae which is well orientated at the molecular level, and a phase in which the structure is less orderly and which cements into a solid fibre, both the fibrillae and the cortical

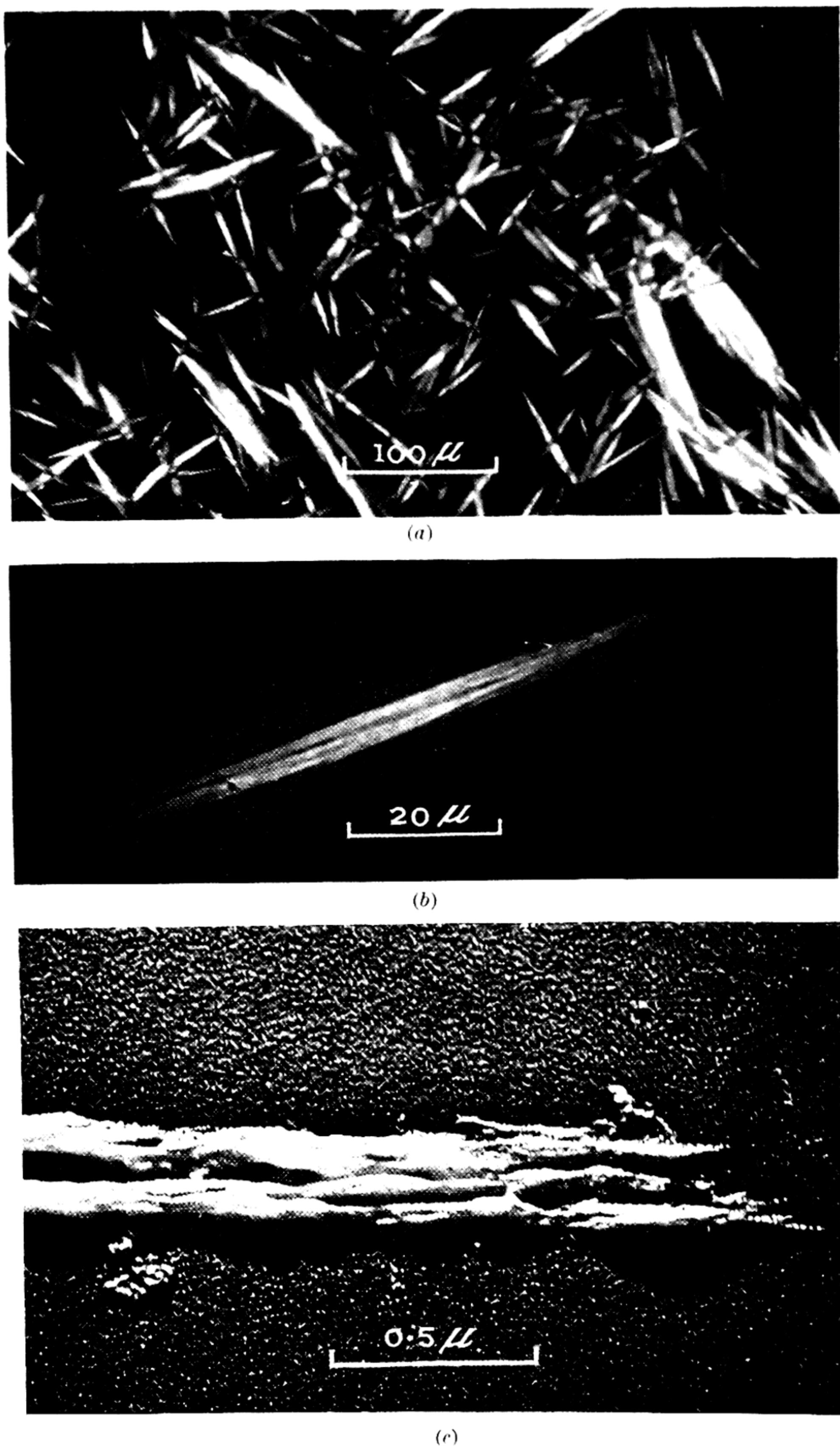


Figure 11.4. (a) Cortical cells retted from Merino wool fibres by trypsin: viewed in polarized light. (H.R.M.) (b) A single cortical cell from the above magnified with higher resolution (N.A. = 1.23) in polarized light. Note the fibrillae that have been exposed by preferential removal of the amorphous keratin in which they were embedded. (H.R.M.) (c) Gold shadowed electron micrograph of fibrils isolated from cortical cells of wool. Note subdivision into tono-fibrils comprised of linearly arranged particles of diameter *circa* 110 Å. Calculated thickness of gold film 9 Å. (From Farrant, Rees and Mercer, *Nature* (1947) 159, 535.)

cells themselves. The fibrillae are more resistant to chemical attack, and are very much more strongly birefringent than the matrix of amorphous keratin in which they are embedded. The striated, fibrillary appearance of cortical cells that have been retted from wool fibres by proteolytic enzymes is probably due to preferential hydrolysis of the amorphous keratin. There are no nuclear remnants in the cortex, but nuclear ghosts are frequently discernible in retted cortical cells because the keratinized material which supplants the nucleus is in a physical state more prone to retting agents than the fibrous keratin that comprises the main part of the cells.

The fibre-cuticle which ensheathes the cortical cells is essentially an envelope of imbricated scales, each the vestige of a single flattened cell which originated from the lower peripheral portion of the bulb and which, during the development of the fibre, keratinized in close continuity with the soft-keratin structures of the inner root-sheath. These scales are isotropic: they have little visible internal structure; they are not birefringent in polarized light; and their x-ray diffraction pattern suggests that the molecules of which they are comprised are disposed more or less at random. The cuticle, as a whole, is much more chemically inert than the cortex; it is comparatively resistant to proteolytic enzymes, and usually persists as a continuous tube if the cortical cells are retted and removed by enzyme action.

There is convincing evidence that the cuticle is comprised of three layers: a very thin epi-cuticular layer, about 100 Å thick, which forms a continuous external covering over the whole cuticle; an exo-cuticular layer situated immediately beneath this membrane; and an endo-cuticular layer which comprises the main mass of the cuticular scales. The outermost, epi-cuticular layer, is extraordinarily resistant to chemical attack and is probably not keratin; the exo-cuticular layer reacts like the less well orientated keratin which binds the cortical cells together, and is comparatively less resistant chemically than the endo-cuticular layer.

THE AMINO-ACID CONSTITUTION OF WOOL KERATIN AND THE SUBSTRATE FOR KERATINIZATION

Studies of some of the more important aspects of the nutritional physiology of wool production depend primarily on a reasonably precise knowledge of the amino acid constitution of wool. While there is no conclusive evidence that wool consists of a protein of definite and unvarying composition, analyses of its hydrolytic products suggest that an overwhelmingly great proportion of the non-medullated wool fibre is comprised of a keratin which has a remarkably constant amino acid constitution. In the cortical cells which comprise the main bulk of the fibre, this keratin is in part highly organized into a semi-

crystalline state that is quite distinct from the amorphous matrix in which the well orientated fibrillae are embedded, and it is probable that these relative degrees of organization are responsible for the small differences in chemical behaviour exhibited by the constituents of the cortex.

The outstanding feature of the keratins, as a class, is their very high content of cystine, and so considerable attention has been given to the sulphur content of wool. The relative constancy of the cystine content of wool keratin has been queried, but as most of the arguments are based on analyses of wools that have been modified by the action of external agencies, they are not cogent from a physiological viewpoint. Fleece grown under natural conditions is subject to wetting by periodic rains, and to intermittent strong irradiation by sunlight; influences that lead to modification of the dithiol linkages, some of which, according to their proximity to other reactive groups in the protein molecule, are particularly labile. Fungal and bacterial attack, oxidative changes, and alkaline conditions all tend to destroy these linkages, and so it is not remarkable that the cystine concentration may differ in various sections along the length of a staple drawn from a fleece. Light and dampness favour oxidative fission of the dithiol linkages which leads to the formation of disulphoxides and finally of the sulphonic derivative, cysteic acid. Alkaline conditions arising from bacterial decomposition of the fatty-acid moiety of the potassium soaps in the suint are at times quite sufficient to effect a considerable amount of cleavage of the dithiol groups with the loss of sulphur and the formation of the symmetrical thio-ether, lanthionine, which sometimes is present as an artifact among the hydrolytic products of wool that has been modified by weathering. In other circumstances the covalent bonding effected through the dithiol linkage may be destroyed altogether; both sulphur atoms are removed to leave two α -amino-acrylic acid residues. The other amino acids are comparatively resistant to these influences.

Medullated wool contains less cystine owing to the dilution of the cortical keratin by the persistence of trichohyaline and of other cellular debris in the core of the fibres. The relatively high concentration of cystine found in cuticular scales that have been prepared by treating the fibres with proteolytic enzymes, however, is not conclusive evidence of hyperkeratinization in the cuticle, as the possibility of preferential removal of amino acids, other than cystine, during the hydrolytic procedures employed for separating the scales is by no means remote.

Although the cortical cells which comprise the greater part of the fully keratinized fibre are bound in a sheath of morphologically distinct cuticular scales, which may differ chemically from the cortex, the considerable differences in the relative proportions of cortex and cuticle in strong and fine wools do not change appreciably the overall

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amino acid constitution which, in freshly grown, normal, non-medullated wools is remarkably constant.

The constitution of the 'bulk proteins' in the leaves of the Spermatophyte plants, which are the natural fodder of grazing animals, is also remarkably constant, although this mixture is comprised of proteins derived from cytoplasmic and nuclear structures. As in the case of the wool fibre, it seems probable that the amino acid constitution of the major part of this mixture of leaf proteins varies little, if at all, and is sufficiently close to that of the minor constituents to buffer the overall composition against small changes in the relative proportions of the mixture. These are somewhat crude generalizations, but they serve to reveal nutritional factors that govern the physiological process of wool production.

The differences between the amino acid content of wool keratin and that of the substrate of amino acids from which it is produced under

TABLE 11.1

AMINO ACID COMPOSITION OF WOOL KERATIN AND OF LEAF PROTEINS

	Wool Keratin*	Plant leaf proteins†		
		Gramineae	Leguminosae	Chenopodiaceae
Glycine	7.2	0.4	—	—
Alanine	4.1	4.4-5.1	—	—
Valine	3.4	3.3-4.2	4.5	—
Leucine isomers	7.2	7.1-8.8	7.3	—
Serine	7.5	—	—	—
Threonine	4.7	3.0	4.0	—
Cystine	9.0	1.3-1.5	1.1-1.3	1.4-1.6
Methionine	0.4	1.4-1.6	1.2-1.4	1.4-1.5
Aspartic acid	4.6	4.9-5.4	4.7-5.4	—
Glutamic acid	8.7	6.6-7.8	6.4-6.7	—
Phenylalanine	1.9	2.5-2.6	2.4	—
Tyrosine	2.0	2.3-2.5	2.3-2.6	2.6-2.7
Tryptophan	0.6	1.8-2.1	1.6-1.9	1.4-1.5
Proline	4.9	3.1	—	—
Lysine	3.2	6.3-6.6	6.4-6.5	6.2-6.8
Arginine	20.0	13.7-14.3	13.0-14.0	12.4-14.1
Histidine	1.1	3.6-3.7	3.8-4.0	—
Amide N	7.0	4.7-5.3	5.1-5.3	5.0-6.0

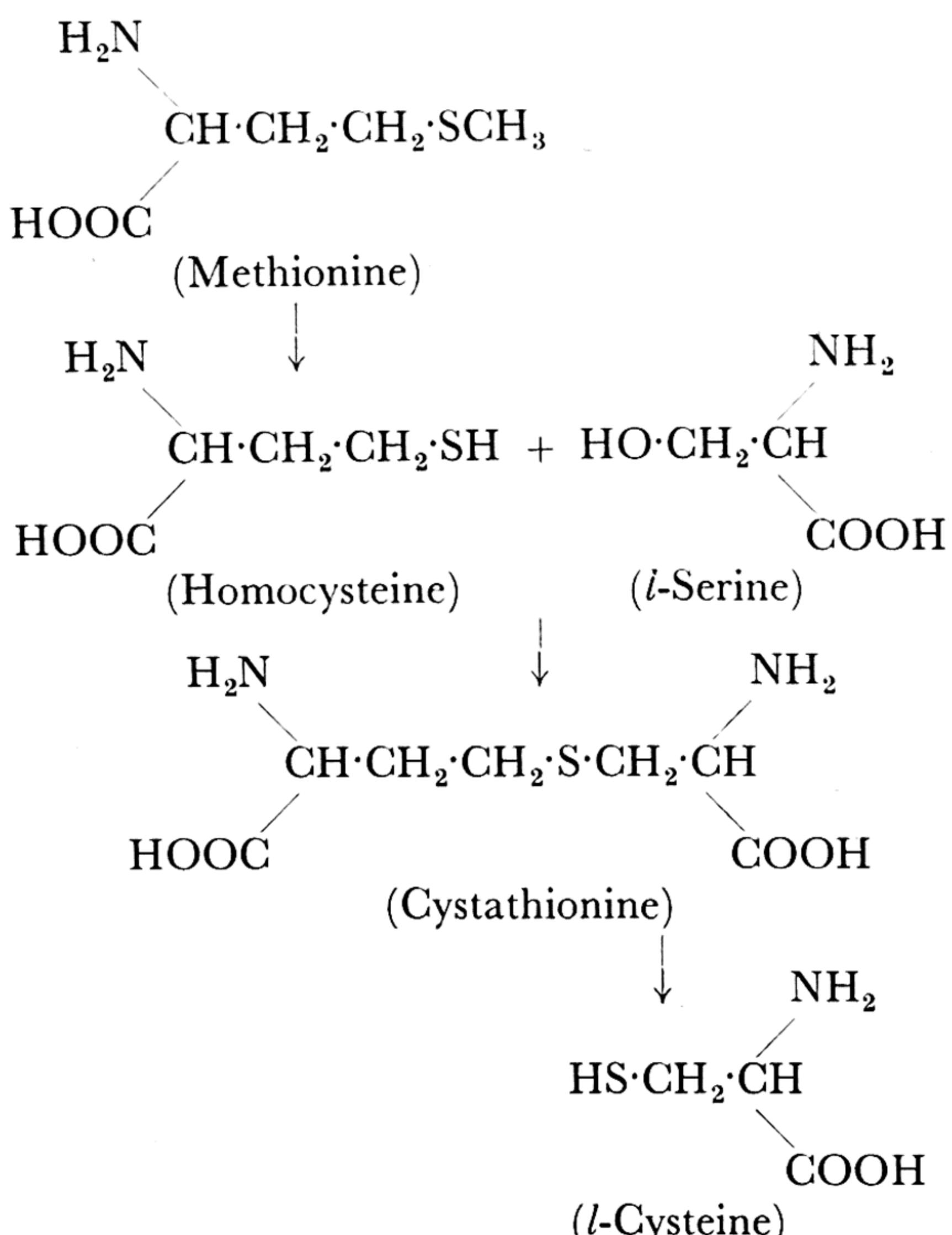
* Wool keratin composition compiled from analyses of Abderhalden and Voitnovici (1907), Marston (1928), Speakman and Townend (1937), Block (1939), Vickery (1940), Martin and Synge (1941).

† Plant protein composition from Lugg (1949). GRAMINEAE : *Dactylis glomerata*, *Lolium perenne*, *Lolium italicum*, *Cynosurus cristatus*, *Festuca rubra*, *Festuca duriuscula*, *Poa trivialis*, *Phleum pratense*, *Phalaris tuberosa*, *Hordeum murinum*, *Zea mays*. LEGUMINOSAE : *Medicago sativa*, *Medicago denticulata*, *Trifolium repens*, *Trifolium pratense*, *Trifolium subterraneum*, *Phaseolus vulgaris*, *Phaseolus multiflorus*. CHENOPODIACEAE : *Atriplex nummularium*, *Spinacea oleracea*, *Beta cicla*.

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natural feeding conditions are set out in Table 11.1. The obvious difference is the very high cystine content of wool keratin: small differences in the concentrations of the essential amino acids, valine, threonine, leucine and isoleucine, phenylalanine, tryptophan, lysine and methionine are not such as might reduce greatly the overall biological value of the plant leaf proteins for wool production. The other amino acids, with the exception of cystine, are of no specific nutritional importance as they are synthesized in animal tissues at a rate commensurate with the needs of the organism and are thus dispensable as such.

The animal's physiological demands for cystine may be met either by cystine (or cysteine) or by methionine. In animal tissues, methionine is convertible to cystine through a metabolic channel in which it is demethylated to homocysteine which then reacts with serine to form the unsymmetrical thio-ether, cystathionine, 11-S- (β -amino- β -carboxyethyl) homocysteine, from which cysteine is produced by hydrolytic cleavage thus:



the net result being an exchange of the thiol group of homocysteine with the hydroxyl group of serine.

The whole of the sulphur in methionine is convertible to cystine *in vivo* and so the capacity of the leaf proteins to provide cystine may be assessed from their content of these sulphur-containing amino acids. The biological value of plant proteins for wool production is limited by their potential cystine content to approximately 30 per cent. This upper limiting value is rarely even remotely approached however: the efficiency with which a highly evolved Merino sheep converts the nitrogen in the proteins of its fodder to wool fleece is usually less than 10 per cent.

Little reliable information is available from which an assessment may be made of the amino acid constitution of the proteins in the micro-organisms that inhabit the rumen. The methionine and cystine contents of the proteins in other classes of bacteria are sufficiently similar to those of the leaf proteins, however, to imply that modification of the plant protein by the activity of the micro-flora in the rumen would not alter materially the amount of sulphur-containing amino acids normally present in the natural fodder. This is largely conjecture, for there is very little exact knowledge of this important aspect of rumination. In certain circumstances microbial synthesis of protein from simple nitrogenous substances may proceed in the rumen at a rate which would provide the animal with useful quantities of protein, but the conditions necessary for this transformation are such as to render doubtful whether the protein in the fodder of a grazing animal is augmented to an important degree by this mechanism.

THE COMPOSITION OF ACCESSORY SECRETIONS IN THE FLEECE

A considerable proportion of the fleece is composed of a fatty material which is generally referred to as the *yolk*. This product of the combined secretions of the sudoriferous and sebaceous glands adheres to the surface of the fibres and may comprise between 20 and 70 per cent of the weight of the fleece. Whereas the composition of the yolk and the amount of it present in a fleece are determined primarily by the heredity of the sheep, they may be influenced to a great extent by the nutritional and physical environments to which the animal has been subjected.

The yolk is separable into two main fractions: the *suint*, a water soluble part, the larger proportion of which is thought to arise from the secretions of the sudoriferous glands; and the *wool-grease*, a fatty part that dissolves in organic solvents, and which arises mainly from the secretions of the sebaceous glands. Apart from extraneous contaminants, there is in the fleece, a third, small and insoluble fraction, made up of epithelial debris comprised of soft-keratin exfoliations from the skin surface, and of the keratinized and semi-keratinized

residua of the inner root-sheaths, which are extruded, together with the fibres and the secretions of the accessory glands, from the orifices of the follicles.

The suint is a mixture of inorganic salts, mainly carbonates, chlorides, sulphates and phosphates of potassium, sodium and magnesium, together with potassium salts of simple volatile fatty-acids, potassium soaps of stearic, oleic and cerotic acids, and a large number of minor constituents, some at least of which are produced by secondary changes subsequent to secretion. The organic fraction of the suint comprises the greater part of the water-soluble portion of the wool-yolk.

There is little or no information in the literature from which a reliable assessment may be made of the approximate composition of the secretions of the sheep's sudoriferous glands. The function of these glands differs quantitatively at least from that of the human sweat glands. The part they play in the heat regulation of the sheep is a minor one as most of the heat exchange between the sheep and its environment is effected by evaporation from the lungs; and there are important physiological differences, as pharmacological evidence suggests that their innervation is quite distinct from that of the sweat-glands of man. Furthermore, the ash of suint contains approximately 50 per cent K_2O , and if this great preponderance of potassium may be taken to indicate the Na:K ratio in the secretion from the sudoriferous glands of the sheep, then the secretion is remarkably different from human sweat in which sodium overwhelmingly predominates.

An outstanding property of the suint is its hygroscopic nature; when in equilibrium with an atmosphere of 100 per cent relative humidity at a temperature of 30°C., suint absorbs about five times its weight of water.

The wool-grease consists, for most part, of waxes—esters of cholesterol and of 'iso-cholesterol' which is a mixture of the triterpene alcohols, lanosterol and agnosterol, and of cetyl-, ceryl-, lanolin-, and other alcohols. The acids with which these alcohols are esterified are distinct from the aliphatic fatty acids usually present in natural glycerides; some of them contain hydroxyl groups, and some have either cyclic or branched carbon chains that are thought to be structurally related to the sterols with which they are combined. Four groups of acids have been identified in wool-wax by modern chemical methods—the normal aliphatic acids of the type $CH_3.(CH_2)_n.COOH$, iso-acids of the type $(CH_3)_2.CH.(CH_2)_n.COOH$, anteiso-d-acids of the type $CH.Me.Et.(CH_2)_n.COOH$, and optically active acids, an example of which is 2-hydroxy-n-hexadecanoic acid, of which approximately 4 per cent has been isolated from wool-wax.

Detailed chemical investigations of the components of the waxes and of other substances present in the fresh secretions of the sheep's sebaceous glands have not been made, and there can be little doubt that some of the very numerous compounds that have been found in wool-grease are the products of secondary changes brought about by the effects of irradiation from sunlight, of atmospheric oxidation, and of bacterial activity to which the fleece is subjected during its growth.

In moist air, the fatty component of wool-yolk oxidizes, more or less rapidly according to its composition, and assumes the dark-brown colour that is familiar in fleeces that have been stored for some years. The 'brightness of the fleece' which is esteemed by wool appraisers, mainly because it implies that the wool may more easily be scoured, is determined by a relative lack of oxidizable constituents in the yolk.

THE INFLUENCE OF NUTRITIONAL LEVEL DURING THE GROWING PERIOD ON THE ULTIMATE WOOL PRODUCING CAPACITY

A sheep that has been stunted by malnutrition clearly cannot express its full hereditary propensity for wool production. However, the fact that the wool-producing capacity of Merino sheep that have been raised under natural conditions of grazing is almost always modified to a greater or less degree by the environment which has prevailed during their development has not been so generally realized. More often than not, the nutritional quality of the fodder available during the first eighteen months of the sheep's life imposes permanent limitations on its subsequent wool producing capacity.

As there are few data in the literature from which a quantitative assessment may be made of the extent of these early nutritional influences, some unpublished findings from a series of experiments that were conducted in this laboratory to determine effects of nutrition on the growth and development of Merino sheep, will be drawn on here to illustrate the nature and degree of the changes that may be encountered in sheep that have been raised in adverse nutritional environments.

The groups of strong-woolled and fine-woolled lambs on which these observations were made were derived from two widely different stud-flocks established in Australia about a century ago. As an entirely different breeding policy had been adopted by each of these studs since its inception, there had been a wide divergence of genotypes, and at this juncture the resulting strains are representative of almost the extremes of the diverse Merino types that have been evolved in Australia. The flock from which the fine-woolled lambs were drawn is of a predominantly Saxon strain, typical of many flocks that have been selected for grazing in the higher rainfall areas. The flock which

provided the strong-woolled lambs is characteristic of the large-framed, plain-bodied strains into whose early Merino-ancestry British long-woolled and other breeds had been introduced, and which had subsequently been selected to provide the physical stamina desirable for the more exacting environment of the arid areas, where to graze the sparse herbage, sheep must of necessity range far from the watering sites. As the former rarely produce twins, the fifteen pairs which comprised the fine-woolled group were, at best, $\frac{1}{2}$ sibs: the fourteen pairs of the strong-woolled group were twins. When these lambs were about 6 weeks of age they were accommodated individually in pens where they remained for the subsequent three and a half years during which the observations and measurements were made. One of each pair was provided *ad lib* with an appropriate fodder of such composition as to ensure a near-maximum growth rate: the other received a ration of the same fodder, the amount being restricted to that which would limit growth rate to about half maximum. Wool production and skin changes in each animal were studied on two rectangular patches, initially 5×10 cm which were delineated by tattooing when the lamb was approximately 6 weeks old, one on either side, each being located in a position where the skin characteristics tend to be intermediate between the extremes found on the skin surface. At intervals of approximately 100 days, measurements of the body dimensions and of the size of the tattooed patches were made; the crop of wool grown on each patch was removed with very fine clippers, and the dry-weight of the clean-scoured fibres and their mean diameter were determined. The density of the follicle population and the ratio of primary and secondary follicles in it at each period were estimated histologically from direct counts made on sections of skin specimens collected by biopsy from the region just anterior to the tattooed area.

Both strains responded similarly to the restricted food intake and so the findings justify tentative conclusions as to how, in general, sheep are affected when their growth is impaired by sub-optimal nutrition. The experimental observations leave no doubt that restriction of the calorific intake during the period of rapid growth and development leads to very significant changes in the skin, quite apart from the delay in development and the changes in the differential growth of the body that are contingent primarily upon skeletal development; and they imply that similar changes would result if growth were impaired by other factors.

Malnutrition lessens the rate of growth of the skin, and because of this the density of the follicle population remains greater. In the growing animal changes in the number of fibres per unit area of skin, however, are the result of two independent variables—the growth of

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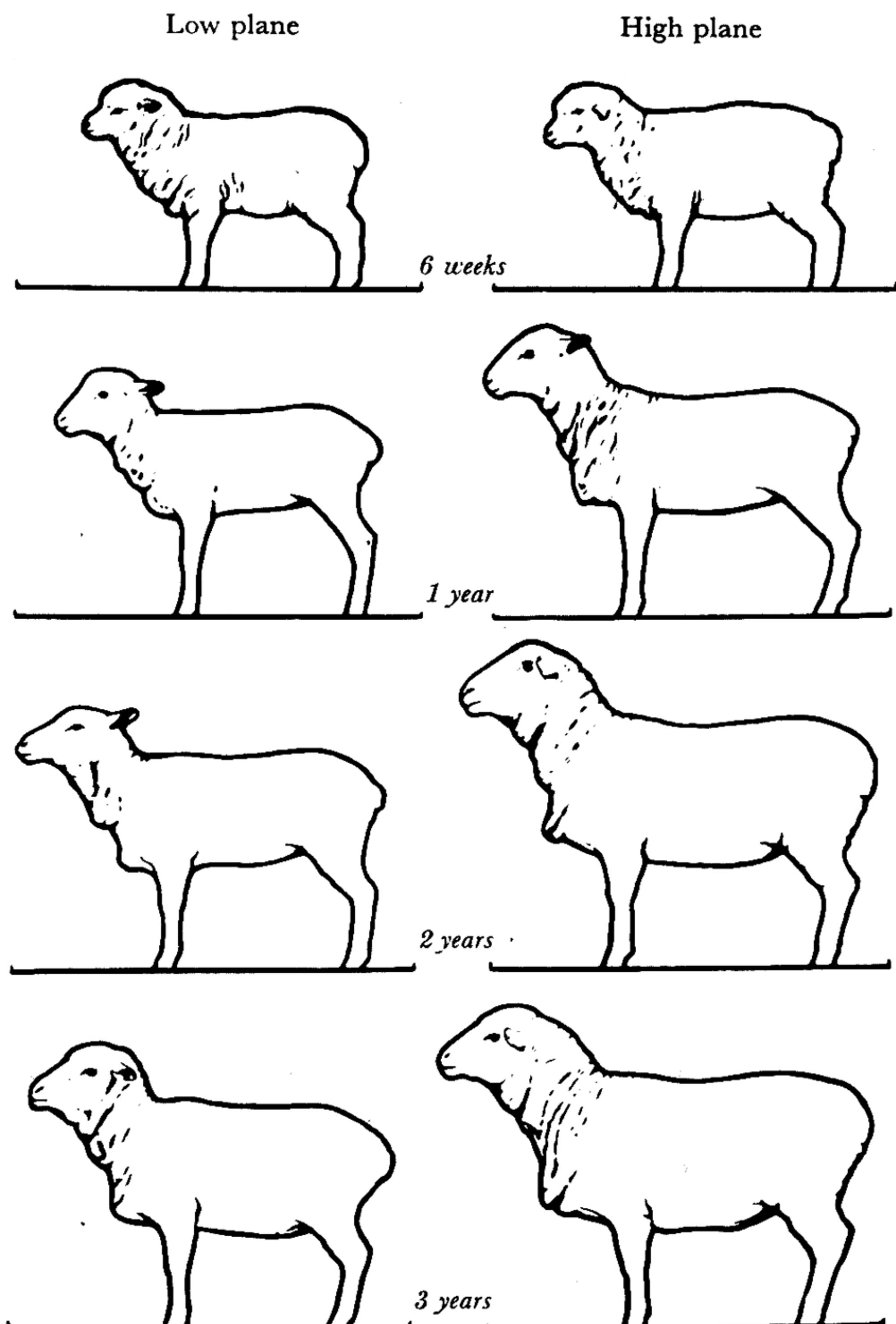


Figure 11.5. The effects of retarding the rate of development of strong-wooled Merino sheep by restricting the food intake are illustrated by outline figures drawn from measurements and photographic records of fourteen pairs of twin lambs which comprised the experimental animals referred to in the text. The high-plane group which consisted of one of each pair, was fed *ad lib* on a near-ideal diet, the low-plane group received the same fodder but the amount of it was rationed to a quantity which allowed growth to proceed at approximately half the maximum rate. Note the relatively juvenile conformation of the mature twin whose development had been retarded. (Del. H. B. Carter from experiments of Marston, Peirce and Carter, 1940-43.)

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the skin, which decreases the follicle density, and the development of new follicles, which increases it. Periodic estimations of the S/P ratio and of the follicle density in skin samples taken from the anterior edge of the patches tattooed on the experimental animals referred to above, indicated that a low nutritional status influences the follicle density in the integument of the growing lamb mainly by changing the rate of skin growth, though the effects on the rate at which new follicles are laid down, and on the final number of follicles that is attained in the integument are quite considerable. The relative extent of these effects may be gathered from the performance of the strong-woolled twins No. 954 and No. 953, the data from which were selected at random to serve here as an illustration of the behaviour typical of the strong-wooled series. At the first observation, three weeks after the beginning of the experimental treatments, the follicle densities in similar regions of their integuments were 120 and 112 follicles/mm² respectively for the near-optimally fed No. 954 and the restricted No. 953; about two years later these densities had fallen to 72 and 96 follicles/mm². During this period the skin areas in the vicinity had increased to 316 and 186 per cent of the original areas, and the S/P ratios implied that by then further differentiation of secondary follicles had augmented the fibre population by 82 and 62 per cent respectively (*cf. Figure 11.1*).

The effects of malnutrition on the body-dimensions, skin growth, and type of wool produced may be gathered from Table 11.2, and *Figure 11.5*. The data are self-explanatory and call for no detailed discussion here. In general, both strains reacted similarly.

TABLE 11.2

THE INFLUENCE OF NUTRITIONAL LEVEL ON THE WOOL GROWING CAPACITY OF
MERINO SHEEP

Period (100 days)	Area of tattooed patch cm ²		Wool produced on patch gm. clean, dry		Mean diameter of fibres μ	
	No. 954 High Plane	No. 953 Low Plane	No. 954 High Plane	No. 953 Low Plane	No. 954 High Plane	No. 953 Low Plane
0	50	50	—	—	22.2 ± .28	20.8 ± .22
1	86	70	9.3	5.1	23.9 ± .29	20.5 ± .19
2	110	77	14.8	5.1	25.7 ± .36	19.4 ± .27
3	132	92	19.1	6.3	28.6 ± .37	22.7 ± .29
4	147	92	22.3	7.9	28.1 ± .34	23.3 ± .30
5	158	93	24.3	7.6	28.7 ± .34	22.3 ± .27

The above data are from twin strong-woolled Merino lambs; No. 954 was fed *ad lib* on a rich diet; the food intake of No. 953 was restricted to approximately half of the quantity that its twin consumed. Treatment began when the twins were approximately 6 weeks of age and was continued for three and a half years. (From unpublished experiments of Marston, Carter and Peirce (1940-4)).

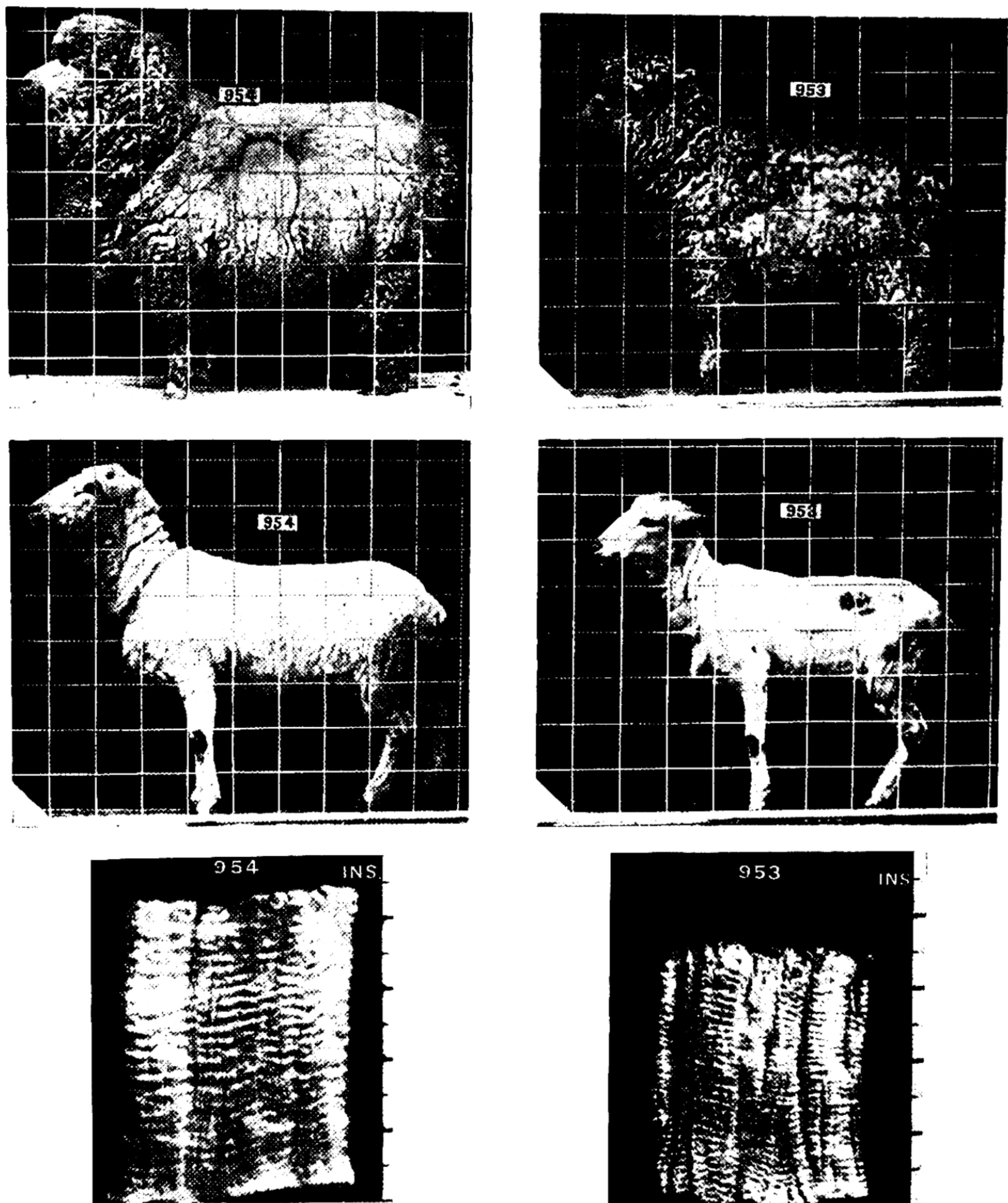


Figure 11.6. The effects of sub-optimum nutrition on the conformation, skin growth, and wool type are illustrated. The strong-wooled ewes No. 954 and No. 953, were twins; the former was fed *ad lib* on a near-ideal diet, and developed at a maximum rate, the latter's development was retarded by restricting the fodder. Treatment commenced when the twins were approximately 6 weeks old; the above photographs were taken about three years later before and after removal of the fleece grown during the year prior to shearing. Note the relative lack of skin development and the juvenile appearance of the stunted animal, and the relative fineness of the wool fleece. (From experiments of Marston, Pierce and Carter, 1940-43.)

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The end-result of a seriously impaired development arising from undernourishment is a smaller, finer woolled adult animal which retains relatively juvenile proportions (*Figure 11.6*), and has a relatively smaller integument in which the total number of follicles is decreased though the distribution of follicles is denser.

The measurements in Table 11.2 express the overall influence of nutritional stress on the quantity and quality of the wool produced by these twins, and are the resultants of a complex set of variables, for in addition to the effects exerted by nutrition on body-size and conformation, and on the relative development of skin structures, which together determine the animal's efficiency as a wool producer, the rate of wool production itself is determined by the quantity and composition of the fodder consumed, quite apart from the sheep's capacity as a converter. Thus although the differences between the wool producing efficiency of the animal which developed in near-ideal nutritional conditions, and that of its twin, which had been stunted by malnutrition, are very considerable, they are exaggerated by the figures that refer to the wool produced during the period while nutritional stress was still being applied.

Nutritional influences on the physiological processes that determine the rate of wool production, irrespective of the overall efficiency of the individual sheep, are best assessed in animals that have reached maturity, for then depletion of the available substrate by other proliferating tissues is minimized.

THE INFLUENCE OF NUTRITION ON THE RATE OF WOOL PRODUCTION

The ultimate nutritional condition that determines the rate of wool growth is, with little doubt, the concentration of essential amino acids in the tissue fluids which surround the wool follicles.

Whereas the supply of this substrate of essential amino acids to the animal itself is determined initially by the quantity and quality of the protein ingested in the fodder, though this supply may in certain circumstances be augmented with amino acids arising from the digestion of proteins elaborated from simple nitrogenous substances by the micro-flora of the rumen, the quota that eventually becomes available to serve the follicles for wool production is determined by interactions of metabolic processes that alter with the nutritional state of the animal.

When the animal's energy requirements are not met completely by the catabolic dehydrogenation of constituents other than the protein in the ration, the amino acids are drawn upon to serve as fuel, and so, according to the extent of the negative energy balance, the

supply available for other purposes is depleted to a greater or less degree. The remaining quota contributes to the pool of amino acids which is in dynamic equilibrium with the proteins of the individual tissues and so is subject to a number of competing syntheses, each of which has a different potential, and each of which is influenced by the overall supply of energy.

Existing knowledge of intermediary metabolism indicates that the synthetic potentials with which the cells of different tissues are endowed, for the replacement of constituents that have been hydrolysed or modified in the normal course of metabolism, for the 'storage of protein' in its classical sense, and for growth and proliferation, differ widely; and the rather diffuse knowledge of the mechanisms which govern growth of tissues in the animal organism suggests that the relative levels of these potentials are poised, in part at least, by endocrine influences. Most, if not all, of what is known of nutritional effects on wool growth can be explained by these interactions. Failure to appreciate the importance of the overall energy transactions, and to realize the effects which these have on the interplay of physiological demands which compete for the amino acid supply, have led to confusing interpretations of the mechanism through which nutrition influences the rate of wool production.

The synthetic potential of the cells of the wool-follicle matrix is high relative to that of the other tissue cells, for the fasting sheep continues to grow wool virtually at the expense of its other tissues, and although in these circumstances the rate of wool production is considerably reduced, it is not greatly less than that which prevails when the animal is provided with just sufficient fodder to maintain itself in energy equilibrium, in which nutritional state the call on the protein in the fodder to serve as fuel is very considerable.

The magnitude of the influence that overall nutritional status has on the rate of wool production may be gathered from the balance sheet, Table 11.3, and *Figure 11.7*. The performance of this animal is typical of that of strong-wooled Merino sheep: the animal, No. 547, was a mature ewe of the same strain as that referred to in the preceding section. Although the rations consumed at the highest level of feeding, period 4, provided abundant energy and close to 100 gm. of available protein/day, which was sufficient to increase the rate of wool production to over four-fold that which prevailed at the level at which the animal was only just maintaining energy equilibrium, period 2, the full wool-producing capacity of this particular sheep had not been reached. Further increase in the protein concentration of the rations under these conditions increases proportionally the rate of wool growth, until, on approaching the physiological limit of the individual's capacity to produce wool, the response to each additional increment of protein decreases according to the law of diminishing returns.

At the highest level of feeding, period 4, when the energy balance was sufficiently positive to minimize the immediate metabolism of amino acids to serve as a source of energy, the amount of amino acids converted to wool protein was only about 7 per cent of the available substrate. It is evident from this balance sheet, that as nitrogen equilibrium had not been achieved in this period, other tissues were drawing extensively on the pool of amino acids, and were competing

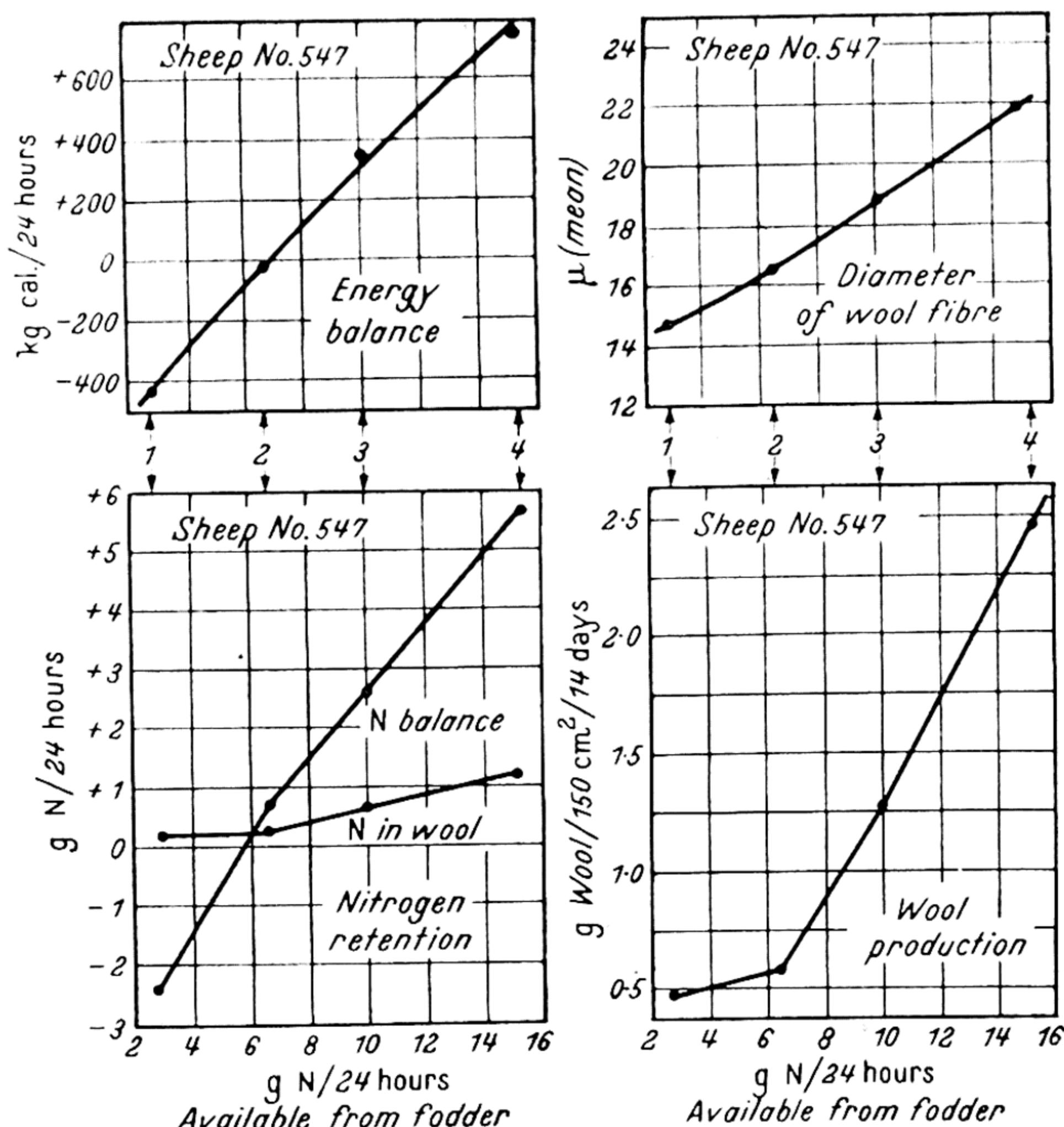


Figure 11.7. The influence of nutritional level on the rate of wool production.

seriously with the follicles. But this competition was only in part responsible for the low efficiency of conversion of the available amino acids to wool protein. In such circumstances as these a limit is imposed by the quantity of sulphur-containing amino acids in the metabolic pool, and so the rate of wool production may be increased materially by augmenting this supply.

The plant protoplasmic proteins have a potential cystine content which is only about one-third of the cystine content of wool keratin and so the peculiar demands of the wool follicles impose an upper limit of approximately 30 per cent on the biological value of these proteins for wool production. This limit is rarely approached even

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by highly efficient wool producers under the most favourable conditions; the efficiency with which a sheep converts the protein in its natural fodder to wool keratin seldom exceeds 10 per cent. In terms of fodder-protein, wool is thus an expensive product.

TABLE 11.3

THE INFLUENCE OF FOOD INTAKE ON WOOL PRODUCTION
MERINO EWE NO. 547, DIET 541

<i>ENERGY TRANSACTIONS</i>				
<i>Combustible energy</i>	<i>Kg. Cal./24 hr.</i>			
	<i>Period 1</i>	<i>Period 2</i>	<i>Period 3</i>	<i>Period 4</i>
in fodder	689	1,395	2,274	3,400
in faeces	129	272	427	676
in urine	56	70	104	129
in methane	73	87	96	94
Energy available	430	965	1,650	2,500
Energy dissipated in metabolism	860	1,000	1,270	1,785
Balance	— 430	— 35	+ 380	+ 715
<i>PROTEIN METABOLISM</i>				
<i>Nitrogen</i>	<i>Gm. N/24 hr.</i>			
	<i>Period 1</i>	<i>Period 2</i>	<i>Period 3</i>	<i>Period 4</i>
in fodder	3.48	7.86	12.51	19.26
in faeces	0.64	1.48	2.53	3.81
in urine	5.45	5.71	7.44	9.77
Nitrogen available	2.84	6.38	9.98	15.45
Nitrogen retained	— 2.61	+ 0.67	+ 2.54	+ 5.68
Nitrogen in wool	0.22	0.28	0.58	1.18
<i>WOOL PRODUCTION</i>				
<i>Gm. clean, dry wool on 150 cm² in 14 days</i>	<i>Period 1</i>	<i>Period 2</i>	<i>Period 3</i>	<i>Period 4</i>
	0.46	0.60	1.22	2.48
Mean diameter of wool (μ)	14.84	16.35	18.84	21.80
S.E.	± 0.60	± 0.73	± 0.76	± 0.80

The amount of metabolizable energy that is called upon to effect the synthesis of wool keratin from its constituent amino acids, although quite small in relation to the overall energy transactions involved in supporting the living processes of the animal, is probably much greater than that implied by the free-energy change, for, *in vivo*, the energy required for this condensation is almost certainly derived from the resonance energy of adenosine triphosphate, the production of which

is expensive in terms of the combustible energy of any particular physiological fuel, and the expenditure of which for protein synthesis is probably wasteful, as there is evidence which suggests that the provision of the free energy increase, of the order of 3 kg. cal/mole necessary to effect the synthesis of a peptide bond from two α -amino acids, involves the release of the whole of the resonance energy of the terminal phosphoric ester group of A.T.P., a quantity which in the environment of living cells is probably in excess of 12 kg. cal/mole.

THE INFLUENCE OF NUTRITIONAL LEVEL ON THE NATURE OF THE WOOL PRODUCED

When a change in the rate of wool growth—which by definition signifies a change in the weight of clean dry wool produced in a unit of time on a defined area of a sheep's integument—is brought about by an alteration of the nutritional status of the animal, changes in both the lengths and cross-sectional areas of the fibres occur. The relationships between these variables and the range over which each responds are individual characteristics of the mature sheep, and, although subject to considerable influence by the animal's early nutritional history, are primarily hereditary traits. In all, they are an expression of the individual's capacity as a wool producer.

The fibre diameters of wool grown under constant nutritional conditions on any particular area of skin are divisible into two populations—a finer, much more numerous class, presumably arising from the secondary follicles, and a stronger, numerically much smaller class, presumably produced by the primary follicles. The latter class adds considerable weight to the fibre-diameter distribution curve and skews its symmetry further towards that of the stronger classes; for this reason, in extreme instances, the curve may become bimodal.

Modifications of these distribution curves brought about by alterations in the nutritional status of the animal are such as to suggest that, under the influence of changing nutritional levels, the characteristics of the two populations may vary independently. As a general rule the finer fibres vary over a more restricted range than the stronger fibres. Within this range each fibre tends to be influenced in proportion to its cross-sectional area.

The response of the fibre diameter to nutritional level is apparent in the distribution curves shown in *Figure 11.8*, which were drawn from measurements of the wool grown on a prescribed area, at two widely different planes of nutrition, by the strong-wooled ewe No. 547 referred to in the preceding section. The obviously skewed symmetry of the fibre diameter distribution of the wool produced at the lower nutritional plane became, typically, more asymmetrical and more platykurtic as the rate of wool growth increased.

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The length of the fibres is similarly influenced by the rate of wool growth though the extent of the change may vary independently of the mean fibre diameter.

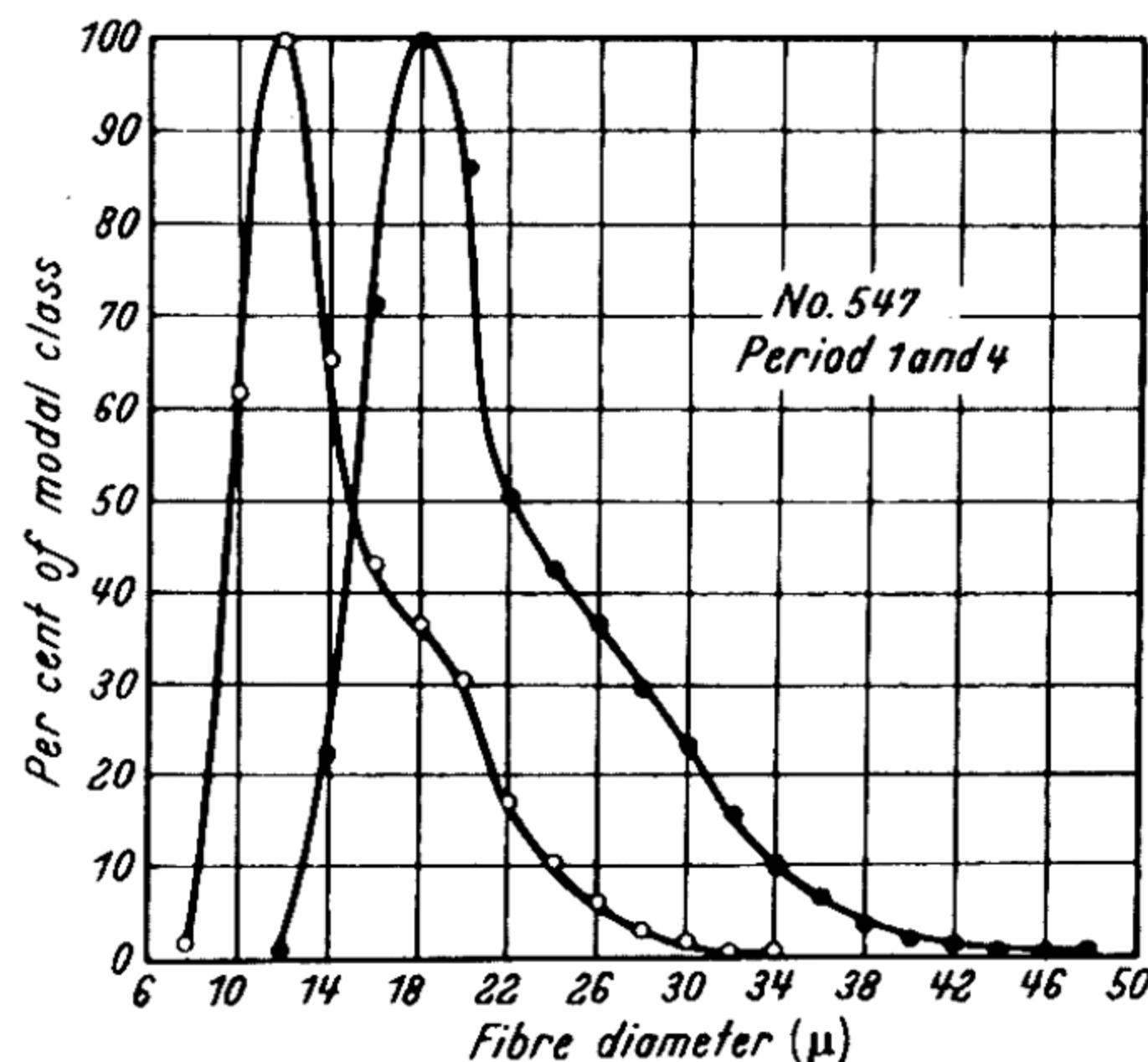


Figure 11.8. The fibre diameter distributions of the wool grown by ewe, No. 547, on an identical region of the skin at two widely different planes of nutrition, indicate the distortion of the normal curve effected by the small but distinct population of stronger fibres. Note the relatively greater response of the stronger fibres to the higher plane of nutrition.

The relationships between the amount of wool produced at any level of nutrition, and the mean diameters and lengths of the fibres seem, in major part, to be due to the structure of the follicles; in particular to the relative size of the bulb and the diameter and extensibility of the orifice at the top of it through which the plastic cell-mass is extruded. The dimensions of the keratinized cells which comprise the fibre remain practically unaltered whatever the size of the fibre. Thus, expansion of the diameter of the fibre must be the consequence of a directly proportional increase in the number of cells in its cross-section. Changes in the rate of wool production effected by nutritional influences may, in consequence, be referred finally to changes in the rate of cell proliferation in the matrix of the bulb, and not to alterations either in the individual size or in the keratinizable contents of these cells.

WOOL PRODUCTION UNDER NATURAL GRAZING CONDITIONS

The above considerations indicate that it is unlikely that a high-producing Merino sheep ever expresses its full capacity to grow wool while grazing on natural pastures, as few pastures, at any stage of

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growth, would be capable of providing the peculiar nutritional requirements necessary to support a maximum rate of wool production. When their protein content is greatest, the fodder plants are young and succulent, and the sward is usually wet; in these circumstances the quantity of available fodder with which a grazing sheep can deal is limited by the water in, and on, the pasture. When the fodder plants dry off, their protein content is low and less easily assimilated from the lignified plant cells. The amount of this relatively indigestible fodder that a sheep would need to consume in order to provide the full complement of amino acids for maximum wool production exceeds the capacity of its digestive organs. Under these extremes of grazing conditions, the situation is at times complicated further by the inability of the sheep to fulfil its energy requirements even when it has fed to repletion; the supply of amino acids which otherwise would provide a substrate for wool production is then drawn on heavily to serve as fuel. The ability of a pasture to provide the nutritional requirements for maximum wool growth, if it were ever capable of achieving this, would, under most Australian conditions of grazing at least, be transitory. The very considerable changes in the rate of wool production that have been observed to supervene on seasonal fluctuations in the composition of the pastures are thus not unexpected. These changes are reflected in the mean diameter of the fibres which vary considerably along the lengths of the wool staples produced by Merino sheep depastured under most, if not all, grazing conditions. The extent of these changes in the fleeces of strong-woolled, high-producing Merinos of the same strain as those whose reactions to controlled nutritional environments have already been briefly discussed in this chapter, indicate that fluctuations of over 400 per cent in the rate of wool production occur between the lush feeding period of late spring and the lean times of late autumn that prevail in southern Australia.

SPECIFIC EFFECTS OF NUTRITIONAL DEFICIENCIES ON WOOL GROWTH

Any metabolic disturbance which reduces food consumption will reflect on the rate of wool growth by diminishing the available substrate, without necessarily having any specific effect on the process of keratinization. In the integuments of laboratory animals the specific lesions that supervene on deficiencies of the vitamins, riboflavine, pyridoxine, biotin and pantothenic acid, seem to be associated with the division and maturation of proliferating cells in the malpighian layers of the epidermis, rather than with the final process of keratinization. Inflammatory dermatitis arising from deficiencies of this nature is unknown in the sheep, as these accessory food factors are synthesized in ample quantity for the animal's needs by the microflora of its alimentary canal.

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A disordered keratinization of soft-keratin, which leads to the distension and blocking of the orifices of hair follicles, is a familiar symptom of an extreme state of vitamin A deficiency in many animals and especially in man. However, this phenomenon, *Keratitis pilaris*, is associated with the new growth that follows the shedding of fibres from the follicles during the course of their cyclic activity; wool follicles produce a continuous filament and are unimpaired in vitamin A deficiency, even when the status of the sheep has been reduced to the extremely low levels at which the terminal nervous symptoms appear.

The only known lesion of nutritional origin which affects directly the metabolic processes entailed in keratinization of the wool fibre is that of copper deficiency.

THE EFFECTS OF COPPER DEFICIENCY ON KERATINIZATION

During the normal course of metabolism, the sheep loses copper by excretion into the lower levels of the intestinal tract from which there is no reabsorption, and so, if the fodder is incapable of making good these losses, the animal's copper status becomes reduced to levels that can no longer meet the full physiological requirements. Deficiency symptoms then appear in an ordered sequence, each reflecting an impairment of one or other of the metabolic processes that require copper for their normal function. The chemical mechanisms involved in the final process of keratinization are particularly sensitive to a shortage of copper, and in consequence, the first obvious sign of a pathologically low copper status in the sheep appears as a marked change in the nature of the wool: the follicles lose their normal ability to impart the characteristic crimp.

During the progressive depletion that ensues when sheep are confined to fodder in which there is insufficient copper to maintain a normal copper status, the critical level, at which the first signs of deficiency appear in the fleece, coincides with a reduction of the copper concentration of the blood to approximately one third of the normal, which ranges about $1\cdot0\text{ }\mu\text{gm. Cu/ml.}$ At this stage the initial signs of the deficiency lesion make their appearance as secondary waves which become impressed over the deteriorating crimps in the newly grown wool (*Figure 11.9(a)*). On further depletion the character of the fleece becomes less and less distinct until the fibres emerge from the follicles as a straight, lustrous growth, entirely devoid of crimp.

These morphological changes in the staple are an invariable consequence of uncomplicated copper deficiency, and they express the decreasing efficiency of a metabolic process within the follicles. On reinstating a normal blood-copper concentration or by applying a

very dilute solution of an ionizable copper salt directly to the skin surface, the ability of the follicles to impart crimp reappears with dramatic suddenness, and the staple which grows subsequently (*Figure 11.10*) resumes the crimp that is characteristic of the particular type of wool normally produced by the individual.

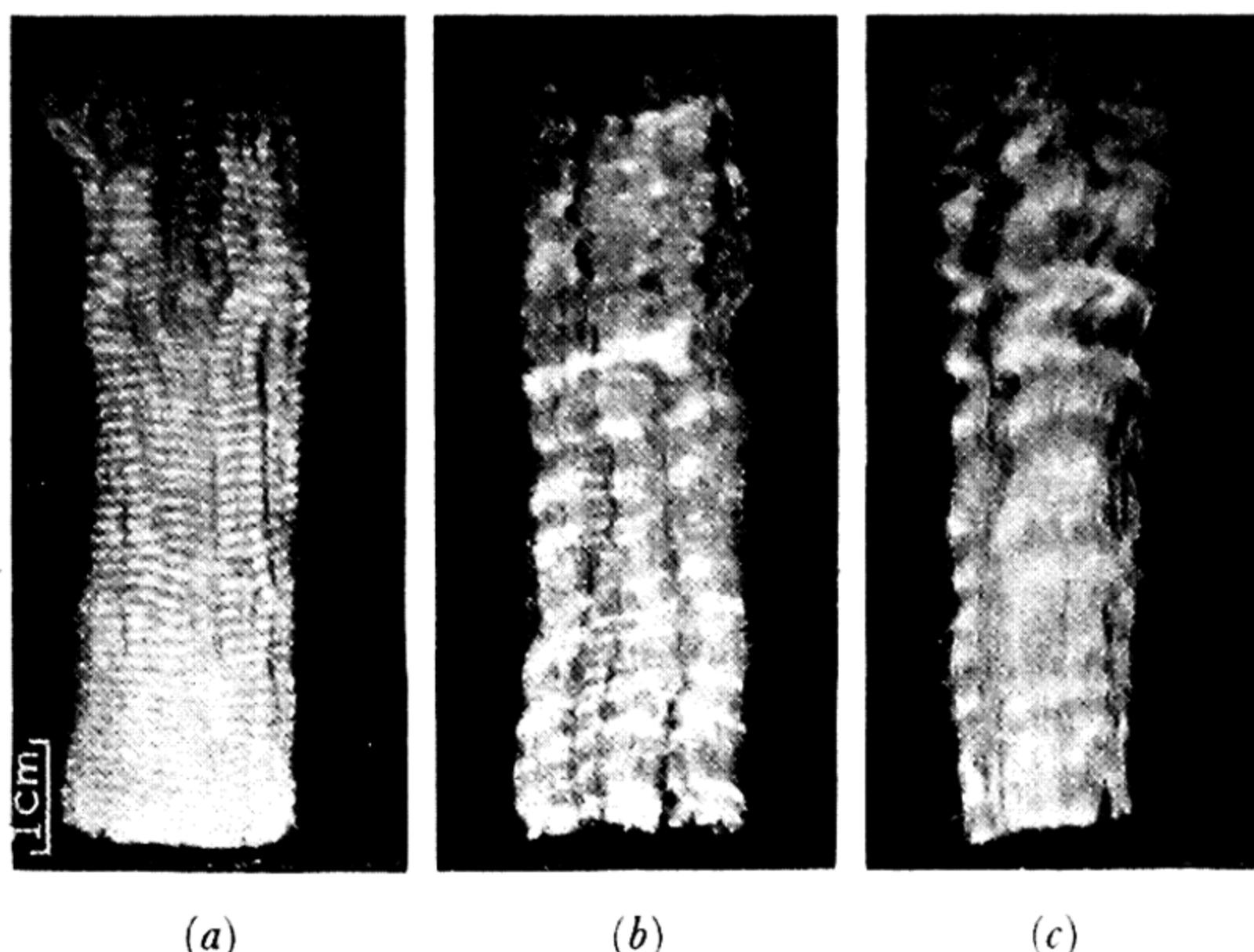


Figure 11.9. Wool follicles lose their capacity to impart crimp when the animal's copper status is depleted below the level that can fulfil the normal requirements. The three staples illustrated were drawn in three successive years from an area defined on the shoulder of a Merino ewe: the first (a) was grown while the animal was on normal pastures, the other two (b) and (c) reflect the deterioration of the animal's copper reserves during two years' grazing on copper-deficient pastures. (From Marston, *Proc. roy. Soc.* (1949) **199A**, 273.)

There is little doubt that the copper-deficient lesions in the wool reflect a break-down of physiological processes within the follicles, which depend directly on the catalytic effect either of copper ions or of copper-containing enzymes. The lesions become apparent early in the course of the copper-deficiency syndrome, and definitely precede the microcytic anaemia and the other effects of disordered iron metabolism which supervene later when the state of the deficiency worsens; they disappear dramatically if the copper status is re-established, and normal function is resumed in the follicles long before there is any marked recession of the other symptoms.

The site of the metabolic break-down that leads to the lesion in the wool fibre is at the level in the follicle where the free thiol groups are converted to dithiol linkages. The free thiol groups of the cysteinyl residues in the reduced protein, which comprises the plastic mass of cortical cells of the developing fibre may be revealed, rather transiently, by treatment with alkaline nitro-prusside or they may be stained permanently by a procedure in which a specific mercaptide-forming

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reagent, 2,2'-dihydroxy-6,6'-dinaphthyl disulphide, reacts with the protein-thiol groups to form a colourless complex that is then converted into an intensely coloured azo dye by coupling with tetra-azotized diortho-anisidine.

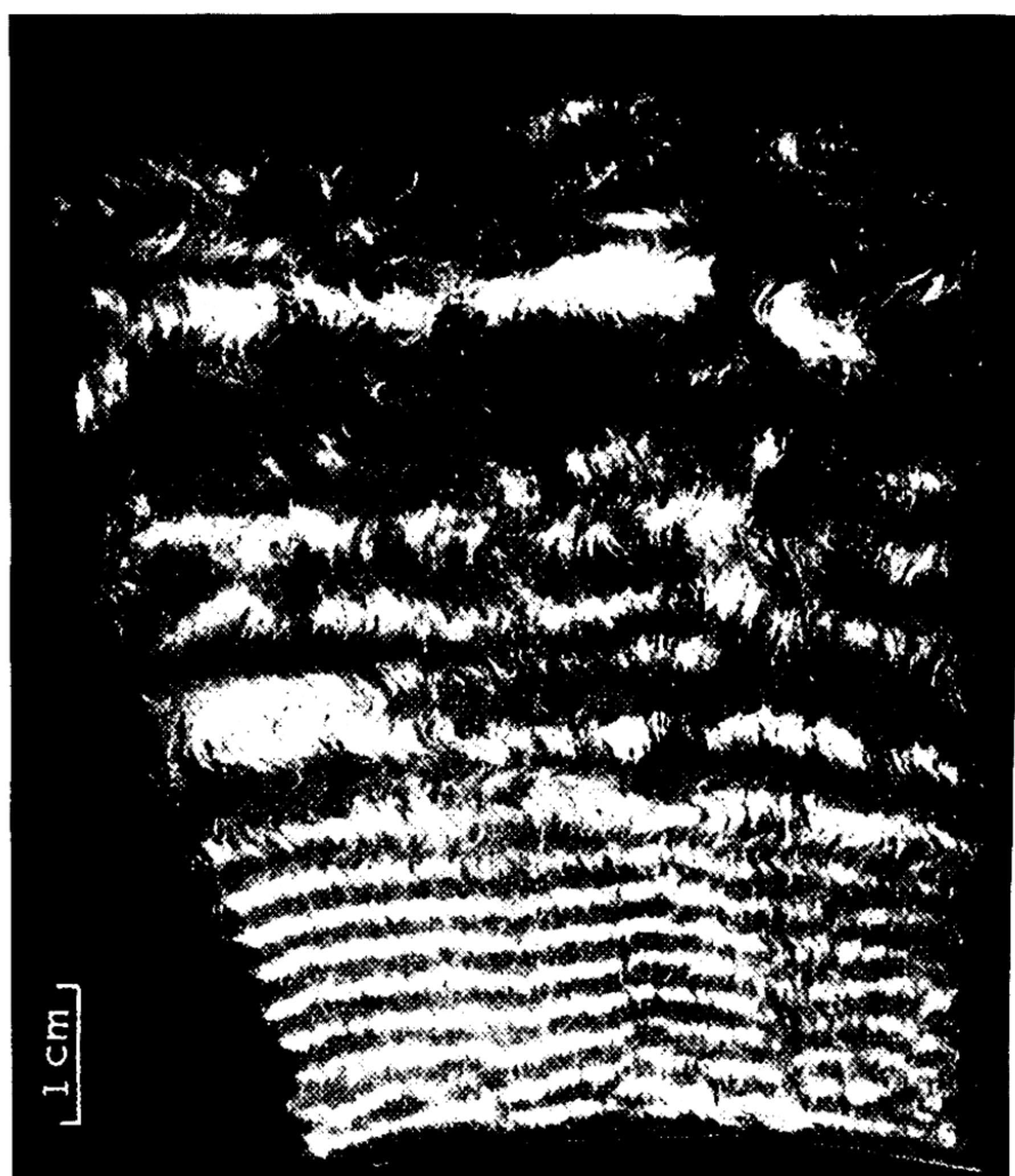


Figure 11.10.—The ability of the copper-deficient follicles to impart crimp to the fibre returns abruptly when the copper necessary for this function is provided. The staple illustrated was taken from an experimental ewe which had been dosed with the equivalent of 10 mg Cu/day while grazing on the deficient pastures on which it had been depleted. (From Marston, *Proc. roy. Soc. (1949)* **199A**, 273.)

In the integument of a Merino sheep that has an adequate copper status, the zone of thiol groups revealed by these procedures begins in the developing fibre just above the neck of the bulb of the follicle, and extends for about 100μ along the shaft before its quite abrupt disappearance indicates that oxidation has completed the keratinization process. In the integument of a Merino sheep that is in a serious state of copper deficiency, this zone begins in the same region of the follicle and extends for $1,000\mu$ or more along the wool fibre. Under these conditions the greater part of the length of the shaft within the

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deficient follicle reacts strongly and the zone of reduction does not end abruptly; the intensity of the reaction becomes progressively less until, about the level where the fibre reaches the skin surface, it is no longer discernible. If a normal copper concentration is reinstated within the tissue fluids surrounding the follicle, this greatly extended zone recedes to its normal dimensions within an hour or so.

During the upward progression of the cell-mass, complete oxidation of the pre-keratin is effected, normally, within 8–12 hours subsequent to the first appearance of thiol groups in the cortical cells. When copper deficiency prevails, the process takes 3 days or more to proceed to completion, and so the fibre retains its plastic condition until it reaches a level quite close to the skin surface.

The preferred molecular orientation of the main bulk of the keratin in the wool fibre originates during the passage of the cells through the constricted neck of the bulb: the cell-mass becomes anisotropic at this level and the asymmetry remains. The fibrillae become aligned parallel to the fibre axis while still in a reduced state, and the relatively rapid copper-catalysed oxidative closure of the adjacent cysteinyl residues tends to fix them in this position. The comparatively slow oxidation which proceeds in the copper-deficient follicles provides ample opportunity for subsequent disorientation before the bonding is completed.

The aberrant physical properties of copper-deficient wool—its reduced tensile strength, its comparative lack of elasticity, its reduced affinity for dyes, etc.—may all arise from a less orderly molecular structure within the fibre. The wide-angle x-ray diffraction patterns, however, are not obviously altered; the main configuration in the copper-deficient fibre is that of the α -keratin of normal wool.

Samples of wool, grown under natural grazing conditions by copper-deficient sheep which were subsequently dosed with copper, revealed, on analysis, no gross variation in the amino acid constitution in the portions of the staples grown immediately before and immediately after resumption of a normal copper status, other than a lowered cystine content in the wool grown while the animals were copper-deficient. This change may well indicate that the deficient wool is more sensitive to chemical modification by weathering. If copper deficiency is found to bring about a lowered cystine content in wool grown under conditions in which there would be little likelihood of cleavage of sulphur by external agencies, some of the hypotheses upon which current theories of keratinization are based would need to be recast.

PIGMENTATION

During the development of follicles that produce pigmented fibres, melanophore cells migrate *via* the papilla to the matrix where they multiply and intermingle with the rapidly dividing follicular cells.

Pigment granules form in the melanophores as discrete particles, about $5\ \mu$ in diameter, and are transferred to the cytoplasm of the follicular cells while these are still in the bulb of the follicle. This transfer is probably effected in a manner similar to that which proceeds in the analogous region of the developing feather, in which the granule-laden dendrites of the melanophores have been observed to pinch off and become engulfed into the cytoplasm of adjacent cells. The distribution of the melanin-containing granules within the cells that later become the cortex of the pigmented fibre is chaotic, until the protofibrils become orientated by extrusion stresses during the passage of the cells through the constricted neck of the bulb; they then become aligned like extended strings of beads between the fibrillae. The particles are relatively inert and so persist in this more or less orderly arrangement throughout the subsequent stages of keratinization.

The process of pigmentation depends on the multiplication of the melanophore cells and on their ability to produce the melanin-containing granules. On first analysis of what is known of the nutritional deficiencies which lead to defective pigmentation in the hair-coats of mammals and in the feathers of birds, it seems reasonable to attribute the depigmentating effects which supervene on deficiencies of biotin, pantothenic acid and pteroyl-glutamic acid, and of zinc, directly to limitations imposed on the multiplication of the chromatophore cells. The striking effects of copper deficiency are more likely to be the consequence of an impairment of the capacity of these cells to produce the melanin pigment; for melanin is known to be formed by the action of copper-containing polyphenol-oxidases on the amino acid, tyrosine.

The effects of copper deficiency on the fleeces of black sheep are spectacular: the follicles lose their ability to impart crimp and to produce pigment. On resumption of a normal copper status, both crimp and pigment appear with dramatic suddenness in the newly grown staple. The probability that both crimp and melanin formation are dependent upon the same enzyme system is remote; in the integument of the guinea pig the follicles that produce black hair contain polyphenol-oxidases which are absent from the follicles which produce white hair, and there are similar differences between the germs of feathers from black and white chickens.

Potentially black sheep that have been depastured on copper-deficient terrain sometimes produce fleeces in which there are sharply defined black bands across the staple; this phenomenon is strongly reminiscent of the alternating black and white pigmentation in the barred feathers of certain birds. Resumption of a normal copper status in sheep which tend to produce banded fleeces results in a continuous production of black wool.

THE CHARACTER OF THE FLEECE: CRIMP AND ITS ORIGIN

Unlike the hairs of most mammals, wool fibres are rarely if ever straight: locks from fleeces of all breeds of sheep tend to be either curled into circular or elliptical spirals or packed into nearly uniplanar waves. The primitive sheep, *Ovis ammon*, *Ovis poli* and their congeners, are exceptional; the coarse, brittle, kemp fibres of their outercoats are practically straight—quite unlike the fine, wavy wool fibres that comprise the somewhat sparse undercoat.

The birth-coats of all lambs of domesticated sheep, those of the Merino as well as those of the British breeds, are made up of curly tufts of fibres, which, according to the breed, vary in size, number, and amplitude. If the follicle distribution on the wool-growing surface is not dense, these whorls continue their growth and develop into locks which retain their original form: thus the mature fleeces of the British long-woollen breeds—those of the Wensleydales, the Lincolns and the Leicesters, for instance—hang down in ringlets that are continuations of the spiral whorls of the lamb-coat. The fleeces from sheep with a somewhat denser follicle distribution—those of the Border-Leicesters are typical of this class—are curled at the tip like those of the true long-woollen breeds, though they tend to assume a wavy, crimp-like form at the base of the staple where the space is more restricted. The Merino, whose wool-bearing surface is particularly closely populated with follicles, produces a fleece in which the fibres become arranged in an ordered mass of apparently uniplanar crimps.

Between the extremes represented by the curled fleeces of the long-woollen breeds and the finely crimped fleeces of the Merinos there is a gradual transition of forms, which, in part at least, is related to the density of the follicle distribution in the integuments. Whatever the final form taken by the fibres *en masse* within the fleece, however, it arises primarily from the tendency of the individual follicles to produce a filament that is either coiled or waved: the spirals, curls, whorls, loose waves, and crimps into which the fibres arrange themselves in the fleece are a secondary result of the adaptation of the twisted fibres to the relatively confined space they occupy.

The most striking feature of the mature Merino fleece is the evenly spaced crimps along the wool staple. The periodicity of these crimps is determined initially by the mean pitch of the waves in the individual fibres, and this is closely correlated with the mean fibre diameter. Because of this relationship, the relative closeness of the crimps in the wool staple is taken by appraisers as a guide in the assessment of the mean fibre diameter upon which the spinning quality of wool primarily depends.

Changes in fibre diameter supervene when the rate of wool production is influenced by an alteration in the level of nutrition, and so considerable variations of the crimp periodicity along the length of the staple are not uncommon in fleeces produced under grazing conditions in which there is a marked seasonal flux and wane in the nutritional quality of the fodder.

Little is known of the physical forces responsible for the orderly distortion of the fibres which ultimately determines crimp. A number of involved hypotheses, which are based on morphological asymmetry of the follicles and on the disposition and orientation of growth gradients within them, have been advanced to explain the phenomenon, but none of them are completely convincing. What is known of the origin of the copper-deficient lesion clearly indicates that the rate at which the final process of keratinization is effected within the follicles determines the nature of the crimp: if the physical forces which are responsible for crimp are to be effective, the fibre must be fully keratinized in the lower levels of the follicle. The final act of keratinization is effected while the plastic mass, which later comprises the fibre, is under tension, and it is conceivable that uneven stresses may be set up which would distort the filament; but why they should lead to a more or less orderly helical growth in some breeds and to a uni-planar crimped growth in others, is not well understood.

THE WOOL FIBRE

Throughout the preceding sections of this chapter, especially in those which discuss the genesis and morphology of wool, it has been stressed that the fibre is comprised essentially of keratin in different states of aggregation. The separate existence of a well ordered phase composed of assemblages of tono-fibrils orientated closely parallel to the fibre axis, and an amorphous matrix in which these fibrils are embedded, is well established and must be postulated in any hypothesis which seeks to explain the physical properties of wool in terms of molecular physics.

When considering fibrous proteins as a class it seems reasonable to attribute the properties they have in common to those of the long polypeptide chains, which are undoubtedly the fundamental structural components of all proteins, and to consider the diversity of properties within the class to arise from individual differences of the amino acid residues in the side groups, the interactions of which might be expected to determine the particular form assumed by the backbone chains.

Knowledge of the relative positions assumed by the macro-molecules in mammalian keratin fibres is based essentially on x-ray diffraction studies, which have indicated that wool and hair are semi-crystalline structures in which the molecular pattern repeats itself most clearly at intervals of 5.1 Å along the axes of the polypeptide chains. On

stretching the fibre to approximately double its length, this pattern is changed completely to a repeated unit of 3.33 Å which is close to the length, 3.5 Å, of an amino acid residue in the polypeptide chain of silk fibroin, and to the effective length of 3.67 Å per residue in a completely extended polypeptide chain. The change from the α -keratin pattern, with a repeating unit of 5.1 Å, to that of β -keratin, with a repeating unit of 3.33 Å, is reversible under certain conditions, though in others, in which liberation of hydrogen-bonding is favoured, the β -pattern may persist on release of the tension. Throughout a cycle of extension and relaxation the 4.65 Å lateral spacing, which is considered to be the distance between the polypeptide chains in the direction of the hydrogen bonded carbonyl and imino groups of adjacent -CO.NH- links, remains unchanged, and the density of the fibre is practically unaltered.

A number of hypotheses have been suggested to explain the reversible changes in the molecular arrangement which take place when the fibre is stretched. The original interpretation, now modified to meet the steric requirements of side-chain packing, considers the 5.1 Å meridional reflexion to be associated with regularly repeated α -folds in the polypeptide chains, each fold involving three amino acid residues; full extension of this pleated structure would imply an elongation of about 96 per cent (1.7 Å to 3.33 Å). An alternative interpretation is based on a molecular configuration which conforms rigorously with structural principles demanded by inter-atomic distances, bond angles, etc., determined experimentally from precise x-ray studies of amino acid and simple peptide crystals, and which accounts for observed and calculated x-ray diffraction maxima in synthetic polypeptides and in proteins such as silk. In this, the α -helix configuration, amino acid residues are orientated in the form of a compound helix which has 3.7 amino acid residues per turn about an axis which itself pursues a helical course with close to twelve times the pitch of the small helices. A structural unit that complies with many features of the meridional patterns of the x-ray reflexions of the α -keratin of hair etc., has been assumed by postulating that six of these helices are twisted, like strands of cordage, about a central helix to make a seven-strand cable.

Neither of these attractive hypotheses accounts for all that is known of the x-ray reflexions of mammalian keratin: the points of difference between the predictions from the suggested models and the observed reflexions seem to be associated with difficulties not only of finding space in any simple compact structure for the relatively massive side groupings of the amino acid residues, but also of deciding the extent of distorting stresses these might induce.

The tensile strength of wool fibres is low compared with that of silk in which the average mass of the amino acid residues is much smaller, and it is especially low compared with that of synthetic fibres in which

molecular packing is close enough to ensure more complete bonding by the cohesive van der Waal's forces and hydrogen bonds. It is probable that keratin fibres would be much weaker than they are were it not for the internal bonding by covalent dithiol linkages. These linkages undoubtedly play an important part in determining the mechanical properties of the fibres: the resistance of a fibre to extension, especially when wet, and its elastic modulus are both very considerably decreased when the dithiol bonds within it are ruptured by chemical means.

The outstanding mechanical property of the mammalian keratins is their long-range extensibility: wool fibres may be stretched to about twice their original length without fracture. When stress is applied, the fibre acts as a rigid body and so obeys Hooke's law until it is stretched beyond approximately 2 per cent of its original length. On increasing the stress, the dry fibre extends, reversibly, a further 20 per cent, with a decrease of entropy, and without very marked change in the α -keratin pattern, other than a slight sharpening of reflexions, which has been ascribed to the unfolding of the chains in the amorphous portion, and to the better aligning of the semi-crystalline fibrillae parallel to the fibre axis. Extension beyond 20 per cent requires the presence of water: there is an increasing resistance to the applied stress, and the x-ray diffraction pattern changes in part from the α - to the β -configuration. Complete transformation to the β -form seemingly involves the hydrolytic cleavage of certain linkages. The break-down may be effected, while the fibre is still under stress, by steaming or by immersion in dilute alkali; in these circumstances further increase of the applied stress will extend the fibre to about double its original length. The fully extended fibre is in a labile state and its subsequent behaviour is determined by the conditions under which the ruptured linkages are permitted to re-establish themselves. If plunged into cold water while the stress is still on, the fibre is set in the elongated form and may be induced to contract only on being reheated in water; if allowed to relax in steam, or in alkali, the fibre becomes super-contracted and assumes a form much shorter than its original length; in this state the x-ray reflexions from it are those of a disordered β -configuration. Super-contraction induced by immersion of the fibre in lithium bromide solution of such concentration as to leave unfilled the hydration shells of the strongly positive lithium ions, is probably due entirely to the rupture of hydrogen bonds, and, under these conditions also, a disordered β -configuration results. When treated with reagents that attack the covalent dithiol linkages the fibres become super-contracted, but contraction under these conditions is accompanied by only a slight disordering of the α -keratin reflexions. Thus it is probable that the characteristic α -keratin structure is determined primarily by intra-molecular hydrogen bonding. This might be expected, as during the

genesis of the keratin fibre, the x-ray reflexions from the strongly reducing, plastic mass of pre-keratin are characteristic of α -keratin, and remain unaltered when the free thiol groups are converted by oxidation to dithiol linkages. The contraction which ensues when the dithiol linkages are broken suggests that the final bonding of the pre-keratin is effected while the mass, which later becomes the fibre, is being subjected to considerable constraint within the follicle.

The shrinkage of woollen fabrics when laundered and the tendency for wool fibres to become progressively entangled into a compact, felted mass when kneaded together in hot water, are closely related phenomena: both are direct consequences of an unsymmetrical friction imparted by the cuticular scales. The resulting uni-directional migration of the individual fibres—‘the root-first creep’—is due, in greater part at least, to the imbrications formed by the overlapping edges of the scales, but it is not merely the result of a progressive movement favoured by the ratchet-like surface of the fibres, as the fibres exhibit unsymmetrical friction against polished glass. Most of the effective ‘anti-shrink’ processes tend to minimize this friction by modifying the free edges of the scales so that they are either eroded away or are masked by decomposition products arising from the chemical processing or by the application of thin films of synthetic resins.

The x-ray diffraction pattern of the α -keratins which comprise mammalian quills, hair, wool, hoofs, horns, claws, etc. is characteristic also of epidermin, the main protein in the epidermis, of myosin and tropomyosin in muscle, and of fibrin and fibrinogen. All of these proteins undergo a reversible α - β transformation of molecular arrangement, and all have a similar capacity for long-range elasticity. In contrast to these, the polypeptide chains in avian and reptilian keratin structures are almost fully extended into the β -form: the repeated units in the keratin of feathers and of the scales of reptiles are 3.1 Å long and may be extended continuously and reversibly to 3.33 Å which is the length of an amino acid residue in fully extended mammalian β -keratin. The polypeptide chains in the collagen fibres of the white connective tissues are virtually inextensible. They are, however, strongly birefringent, and the most important feature of their x-ray diffraction pattern is a meridional spacing of 2.86 Å.

Studies of these relationships which began originally with investigations of the molecular configuration in the textile fibres silk and wool, have received a new stimulus from the recently propounded α -helix hypothesis of protein structure; and perhaps it is not too hopeful to expect in the near future further clarification of the structure of fibrous proteins.

ANIMAL BEHAVIOUR

CHAPTER 12

THE BEHAVIOUR OF GRAZING ANIMALS

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THE STUDY of animal behaviour holds the unique position of being both the oldest art and the youngest science in agriculture. The antiquity of the subject scarcely needs any emphasis. Without an amazingly intimate knowledge of the behaviour of the animals which hunted him, as well as of those which he in turn hunted, primitive man could not have survived. Similarly his attempts to domesticate wild animals could not have succeeded. In fact it has been claimed that the biological sciences as we know them are but the logical development of the original behaviour observations of our distant ancestors. It is, therefore, all the more surprising that behaviour studies should only now be receiving scientific recognition and should still be looked upon as a novelty by many agricultural and veterinary scientists.

During the past twenty or thirty years, however, the subject has been enjoying the attention of agriculturalists in increasingly large numbers and, whereas a few years ago such studies were the preserve of a minority of enthusiasts, who managed to include them unofficially in a quite different programme of research, there are now, in all parts of the world, groups of workers in research institutes and universities tackling behaviour problems with the official blessings of the authorities. It is perhaps curious that the initiative in this development has been with the agronomists and not with the animal physiologists whose training and interests would more appropriately have fitted them for the job.

The pasture research workers have, during the past fifty years, revolutionized agricultural thought and practice by their fundamental researches into the establishment and management of leys, and they have now indicated that while existing experimental evidence on the breaking up, establishment, and improvement of grassland is, on the whole, reliable and it is possible to advocate with confidence the species and strains of herbage plants which are suitable for a particular environment, and to compound them into suitable seed mixtures, we are, nevertheless, remarkably ignorant of the part which is, or should be, played by the grazing animal in the determination of suitable practices of grazing management. As Sir George Stapledon has pointed out, 'so intimate is the connection between the grassland

complex and all its reactions, and the grazing animal complex and all its reactions, that it appears obvious that it is not possible to understand the one complex without also understanding the other'. While the pasture complex has enjoyed the attention of an increasingly large number of workers for a large number of years, and has generously rewarded them with a considerable mass of information, it is, on the other hand, difficult at the moment even to define the animal complex. Its component parts will certainly include such factors as the animal's weight, age, sex, health, efficiency of digestion and efficiency of metabolism, and to these must be added the animal's behaviour.

Certainly since the end of the last century many attempts have been made to assess the feeding value of grassland by chemical methods but the inadequacy of existing empirical methods of herbage analysis is now well recognized, and the tendency when considering the quality of grass to look chiefly at the nitrogen content and to imply that young grass is so much better than mature only because of its higher protein content is to be deplored. There exists a real need for a further study of the energy supplying constituents which together comprise by far the greatest proportions of feeds, an examination of their relative availabilities, and a study of management practices which will maintain a profitable compromise between yield and quality. The digestion and utilization of grass is clearly the vital phase in the grassland cycle since it is upon these processes that animal production directly depends. Before, however, determining the digestibility and utilization of a diet by an animal we must first know the qualitative and quantitative composition of the diet. From the experimenter's point of view this at once highlights the essential difference between grass and other feeding-stuffs. With the other miscellaneous concentrates and roughages the composition of the ration consumed can be controlled by man, but with grass this is, in the greater part, determined by the self-selection of the grazing animal. Hence in our investigation of the animal complex one of the first questions which needs to be answered is 'what does a grazing animal eat?' and linked with that 'what are the factors which govern this selection?' However, before these questions can be fully answered we need to have an appreciation of the general behaviour pattern of the grazing animal and the factors influencing it, in other words to discover the 'how', 'when', and 'where' of grazing as well as the 'what' and 'why'.

THE GENERAL BEHAVIOUR PATTERN OF GRAZING ANIMALS

Valid and standardized techniques are the prerequisite of any scientific investigation. It is an important criticism of grazing behaviour studies in all parts of the world that there is no standardized

technique of observation and no comparison has yet been made of the accuracy of the many different methods now used. There is, for instance, no uniformity concerning even the period during which observation should be made.

Some workers have mistakenly assumed that during the hours of darkness animals will remain at rest and they have therefore only recorded their observations during the hours of daylight. Others have recorded continuously for twenty-four hours and some have even watched for as long as seventy-two hours without a break.

Similarly methods of recording may vary considerably. Some workers record the behaviour of individual animals while others record the behaviour of flocks or herds. Some workers make a continuous recording while others only record observations taken at regular and frequent intervals. Some records are the work of single observers while others are made by several observers working a shift system. Until investigations have been made to assess the comparative reliability of these various techniques it is not possible to explain satisfactorily the different results which have been reported.

In an effort to increase the accuracy of behaviour records a number of automatic and semi-automatic recorders have been evolved. For use with animals housed in pens or stalls these auto-recording machines have proved very successful and with their use J. G. Gordon, working at the Rowett Research Institute, near Aberdeen, has been able to record in extreme detail and with every accuracy the activities of penned sheep over continuous periods of 150 hours. The difficulties of using such machines to record grazing behaviour are, of course, much greater and have not yet been overcome. However, BURTON and CASTLE (1950) have described the construction and use of portable infra-red ray equipment for animal observation in the field. For watching, from a stationary position, not more than four animals at a range of ten to fifteen yards on a clear dark night, the equipment was ideal. When using it to observe a large number of animals, either in the field or in the cowshed, the observer was liable to miscount the animals owing to the limited field of the screen. Also the constant wearing of the equipment, which weighed twenty-one pounds, was very tiring and when misty the lenses quickly clouded over.

That there exist important differences between the behaviour patterns described by various workers is not surprising. In addition to the discrepancies due to differences in observational techniques, there is a complex of environmental factors which must be expected to influence critically a 'normal' pattern of behaviour. For example such variable factors as the climate, the density and quality of the sward, the size of paddock, the system of grazing management, and, of course, the individuality of the grazing animal may all influence very

significantly the times devoted to different activities. Nevertheless there are certain general features which appear to be common to the behaviour patterns of all grazing animals.

Of the time devoted to grazing about 65 per cent occurs during the hours of daylight and 35 per cent when it is dark. As one would expect, more time is spent grazing in darkness during the winter when the hours of daylight are reduced. Since so much time may be devoted to grazing during the hours of darkness it follows that the type and quality of pasture available at night should ideally be approximately the same as that used during the daytime. Certainly the use of small, so-called night pastures should be discouraged. Almost invariably the pattern of behaviour shows a rhythmic periodicity in which fairly long periods of intensive grazing are followed by shorter periods of idling, rumination, and rest. The two most intensive periods of grazing occur at daybreak and sunset but there are normally six or eight grazing periods during every twenty-four hours. It is possible that this fact has an important bearing on the methods which are used in herbage digestibility studies. GORDON and TRIBE (1952) have reported that Cheviot ewes gave greater bodyweight gains and an increased efficiency of food utilization when offered their daily ration in eight small feeds than when given the same quantity and quality of food in one large feed. This finding, coupled with the fact that, when freely grazing, animals do divide their daily ration into as many as eight feeds, suggests that cut herbage should be fed in this manner to housed animals in experimental work of a physiological or nutritional nature. Bearing in mind the dangers of generalizing one can say that a cow spends about eight hours each day in grazing, while a sheep will average as much as nine and a half hours when grazing under similar conditions.

It is during the hours of darkness that the animal does most of its rumination. The peak of ruminating activity usually takes place soon after nightfall but if ruminating animals are disturbed they will revert either to idling or, very probably, to grazing. It is noticeable that whereas the change from ruminating to grazing may be abrupt and immediate, animals never change from grazing to ruminating without first spending some time idling or at rest. The time devoted each day to ruminating, mostly when the animal is lying down, is approximately three-quarters of that spent in grazing.

It is debatable whether cows and sheep, when at rest, ever sleep. It is very doubtful whether one can decide this question by observation alone, but it is certain that these animals seldom close their eyes and when they do so it is only for a very few minutes at a time.

The various factors which may have an important influence on a 'normal' behaviour pattern are best considered individually.

Climate

It is sometimes difficult to differentiate between the effect on grazing behaviour of particular weather conditions and the effect of the changes in the quantity and quality of the sward which may accompany a changed climate. However, some workers (*e.g.* SEATH and MILLER, 1947) have shown how extremes of temperature may alter behaviour (*see* Chapter 6).

Hot weather causes animals both to graze for a shorter time than normal and to increase the proportion of time that is spent grazing during the night. When idling under these conditions the animals appear agitated and seldom rest for long periods and in consequence the distances travelled tend to increase. Similarly the number of times an animal drinks, defecates and urinates all tend to increase. As might be expected these effects are less apparent in those breeds of cattle which are commonly found in the tropics such as the Afrikaner than they are in others which are indigenous to temperate climates, such as the Shorthorn or the Aberdeen Angus.

During cold, windy, or rainy weather grazing times are again shortened and the normal overall pattern may be radically altered. Grazing will be most intensive during the periods between showers or storms, irrespective of the time of day or night. When a storm begins animals will usually cease grazing and walk to shelter if such is close at hand, otherwise they will stand with their heads down wind. Under such conditions hill sheep and cattle will move to higher ground. When the weather is wet it has been observed that the animals will drink little or no water.

The Type of Sward

Grazing habits are very sensitive to changes in pasture quality and quantity. Generally the factors of quality and quantity are inter-dependent but under some conditions, *e.g.* those occurring under systems of strip grazing management, the quantity of herbage on offer can be maintained at a consistently high level and only the variations in herbage quality will influence the animal's behaviour. These conditions have been discussed by WAITE, MACDONALD and HOLMES (1951) who showed that a close correlation exists between an animal's intake of herbage, on a fresh weight basis, and the time it spends grazing. Therefore, since cows require approximately one and a half times as much young leafy herbage to satisfy them as of stemmier, more mature, material, they spend a longer time grazing on young, luscious herbage than they do on less leafy, higher fibre material. It has been suggested that the reason for this may lie in the fact that it is very probable that the rate of passage of short succulent grass through the alimentary tract is more rapid than that of longer, relatively dry grass. The ingestion of long portions of stemmy herbage may result

in a less densely packed mass in the rumen and perhaps an earlier sense of repletion after eating a relatively small weight of fresh material. If this assumption should be proved valid then it follows that the amount of grass eaten during grazing is not entirely dependent on its chemical composition or nutritive value *per se*.

The general importance and interdependability of quantity and quality have been discussed by HANCOCK (1950). He has shown that the two activities most influenced by changes in the nature of the sward are grazing and ruminating. Since these activities are themselves interdependent, and under some conditions mutually restrictive, he has computed a ratio, ruminating time : grazing time, which he calls the *rt/gt* value. Numerous observations published since Hancock's paper appeared have necessitated some revision of his original thesis and in our present state of fuller, yet still incomplete, knowledge the following tentative conclusions seem to be permissible. Abundant pasture, per cow as well as per acre, results in a comparatively long grazing time coupled with a short ruminating time if the quality is high, but a short grazing time with a long ruminating time if the quality is poor. The *rt/gt* value is thus very low in the first case and high in the second. Quantitatively poor pastures result in invariably long grazing times and short ruminating times when the pasture is good, making the *rt/gt* value low, and longer ruminating times when the pasture is poor, making the *rt/gt* value high. The suggestion that the efficiency of a sward for animal production may be assessed by calculating the appropriate *rt/gt* value is theoretically true for it may be argued that the lower the value the better the sward, but in practice swards may vary so much between the easily defined extremes of good and bad quality, and high and low density, that the *rt/gt* value is probably not a sufficiently sensitive yardstick to differentiate between most of them. However, it is still true that animals generally have to work longer hours under adverse grazing conditions since the periods spent grazing or ruminating, or both, are then longer than when the pasture quality and quantity are optimal.

Size of Pasture

It has been shown on several occasions that the size of the pasture available to the grazing animal will influence its behaviour and in particular the daily distance that it travels. In general one can say that the bigger the area of the pasture the farther will an animal walk. SHEPPERD (1921), for example, reported that beef cattle on a 30-acre pasture walked $1\frac{1}{2}$ miles between four o'clock in the morning and eight o'clock at night whereas similar cattle throughout the same period travelled $3\frac{1}{16}$ miles on a 100-acre pasture, and $5\frac{1}{2}$ miles on a 640-acre pasture. There must obviously be a limit to this tendency at both ends of the scale, but so far they have not been established.

The System of Management

The influence of a particular method of grazing management on the behaviour of grazing animals is often very marked but may frequently be due more directly to the effects of pasture type which, in turn, may be the intended result of a particular management system. Under conditions of extensive grazing, *e.g.* on mountain and moorland farms, it is often difficult to determine exactly how an animal's behaviour is influenced by the management practices. It is in these cases that the behaviour of both animal communities and individuals most closely resembles that of undomesticated animals, and behaviour may be broadly classified under one or other of the three headings, sexual, nutritional and self-preservational. In the case of the intensively managed animal, the sexual drive is only allowed relief under the circumscribed conditions set up by man, and the animal has no concern of self-preservation since this responsibility is now met by husbandmen, trained dogs and fences.

With both extensively and intensively managed animals a very marked change may be made in their nutritional behaviour by feeding some form of supplement. It has often been recorded that such a supplement will reduce the times spent grazing and increase those spent idling and resting. Under some conditions, *e.g.* the intensive grazing of high yielding dairy cows, this may be a desirable result since the object here is to achieve the very maximum daily intake of digestible nutrients and thus too much bulky herbage is a disadvantage. Under other conditions, however, this marked tendency to reduce grazing times may have serious consequences. The most important characteristic of hill cattle and sheep is their hardiness which includes their ability to forage for food in extremely poor pasture and climatic conditions. Experience has shown that if a supplement is regularly and frequently fed to such animals they show a diminished inclination to forage for themselves and, if for some reason supplementary feeding subsequently has to stop, the animals then fail to withstand the rigorous hill conditions as well as animals who have never been fed a supplement at all. In this connection a series of experimental observations carried out on hill sheep are of interest (TRIBE, 1950a). Two comparable groups each of twenty-five Scottish Blackface sheep, one of which received a daily supplement and one of which did not, were observed grazing firstly in neighbouring fields of comparable size and botanical composition, and secondly in the same field. When the two groups grazed separately the supplemented animals spent less time grazing and more time resting than the unsupplemented group. When the two groups grazed together their grazing and resting times were very similar and represented those of the unsupplemented group when grazed alone. It is of interest that this phenomenon of social

facilitation has also been reported in such widely differing species as fish, rats and apes. This type of behaviour, incidentally, is of considerable importance from an experimental as well as from a practical point of view. It is incorrect to assume that by giving a dietary supplement to one set of grazing animals it is always possible to raise their nutritional plane by that amount above another unsupplemented group unless all the animals are grazing together. To give a supplement to a whole flock or herd of grazing animals merely means that a shorter time will be spent grazing.

Many workers have reported how differences in managing intensively grazed animals may result in different behaviour patterns. For instance it is known that sheep graze for a shorter period on good temporary pasture than they do on permanent pasture, and that they spend even longer still in grazing on rough marginal pastures. When comparing the behaviour of rotationally and continuously grazed cows, HODGSON (1933) found that the former grazed for less time than the latter. As the season advanced the rotationally grazed cattle spent less time grazing and a greater time lying down while the continuously grazed animals reacted in a reverse manner. The results of ATKESON, SHAW and CAVE (1942) confirm these findings for when they observed cattle throughout an "animal-day" of almost twelve hours they found that on good pasture the cattle grazed an average of 5.6 hours, on medium quality pasture 6.5 hours, and on poor pasture 7.3 hours. It has been suggested that this tendency is only evident within certain limits for there must come a point when grazing times are limited by a fatigued musculature of the jaw. The suggestion of JOHNSTONE-WALLACE (1948) that in the case of cattle this limit is reached in eight hours has subsequently been shown to be mistaken and reports of grazing times as long as nine or ten hours are by no means uncommon.

Although grazing times tend to decrease as the quality and quantity of the pasture increases and, therefore, it may be assumed, as the intensity of the sward management increases, there comes a time when the reverse is true. In their comparison of the behaviour of rotationally and strip grazed dairy cattle, Waite and his co-workers (1951) found that shorter grazing times were returned by the rotationally grazed group. This was probably because the more closely-folded cattle had no opportunity for selection and grazed all the herbage on offer more closely than the others. To graze pasture which consists mainly of defoliated stems to within an inch or two of the ground presumably takes more time and energy than eating merely the leafier portions. It is of interest that Waite's rotationally grazed cattle remained in the same paddock for four days and their average daily grazing times increased from 7.7 hours on the first day to 9.8 hours on the fourth day. These results support the suggested explanation of the

longer grazing time by the close-folded animals, more time being required as soon as the easily torn leaf has been removed.

Individuality

Perhaps the greatest and most imponderable problem which besets the animal watcher is the degree to which recorded behaviour may be due to any of the environmental factors already discussed and how far it is due merely to 'the personal whim of the animal'. In order to clarify the concept of individuality as far as grazing behaviour is concerned HANCOCK (1950b), working at the Ruakura Animal Research Station in New Zealand, conducted a series of observations in which he employed a number of sets of monozygotic twin cattle.

The difference between sets of twins reflected the inherited variability in grazing behaviour and an analysis of his results showed that this was by far the largest source of variation due to individuality. A part of these inherited differences could be explained by relating them to differences between the physiological requirements of individual animals. It seems reasonable to argue that increased nutritional requirements during growth, pregnancy or lactation result in an increased food intake and, therefore, in increased grazing and ruminating times. It is, however, important that these relationships between nutritional need, food intake, and grazing behaviour are by no means rigid or perfect. Several workers have reported, for instance, that production, *e.g.* milk yield, cannot be directly related to the length of time spent grazing, and in New Zealand it has been shown that in many cases dry-matter intakes are not proportionate to grazing or ruminating times. The reason for this is probably that individual animals, due to their genetical composition, vary in their efficiency as grazers and that, therefore, their herbage intake per minute of grazing may vary within quite wide limits. The factors which determine an animal's grazing efficiency are such anatomical characteristics as narrowness or shortness of the lower jaw, which may result in either fewer bites per minute or a smaller intake per bite, and the degree of selectivity shown by each animal. The degree of selectivity may be represented statistically by the number of bites taken per minute and this may vary considerably between individuals. Whether a high degree of selectivity, and, therefore, a low number of bites per minute, should be taken as a criterion of a high or a low efficiency of grazing depends upon the nature of the available grazing. When dealing with a relatively dense sward of mixed quality the selective grazer is at an advantage since it will choose a higher proportion of the leafier and more succulent herbage and so achieve a high intake of digestible nutrients. On quantitatively poor pastures, on the other hand, the selective grazer may spend such a long time in the selection as opposed

to the actual collection of food that when its limit of grazing endurance has been reached it will not have ingested so great a quantity of nutrients as the animal which is not so fastidious. Inherited individuality has also been shown to influence the distance animals walk, the frequency of drinks, defecations and micturitions, and also the speed of rumination, number of bites per bolus and the length of rumination periods.

From this general discussion of the more important factors which may influence the results of grazing behaviour investigations it is evident that a good deal of restraint must be exercised on the tendency to draw rather wide conclusions from them. Certainly the general application in different environments of one particular set of results is not justifiable. With this necessary limitation in mind it is nevertheless true to say that within the circumscribed conditions of a particular investigation the results obtained from animals watching may be of the greatest value.

As in all fields of agricultural research, the object of grazing behaviour studies with domestic stock is eventually an increased efficiency of animal production. It may be legitimately argued that a fundamental understanding of behaviour will ultimately lead to improved methods of animal management for optimal production since 'a fuller knowledge gives a fuller control'. However, it must be remembered that this is not the only way of gaining a 'fuller knowledge', and, from a short term view at any rate, it is possible that other types of animal experimentation will give better dividends in terms of animal production. This does not mean that behaviour studies have no application in animal husbandry in the near future. When carrying out animal production trials it is frequently necessary to make behaviour observations before the results are fully understandable. For example, LEVY (1935) used this technique in New Zealand when solving the problem of feed flavour in butter. He showed that because cows under his conditions grazed little between midnight and morning milking feed taint in cream could be avoided by grazing those pastures responsible for it during the night. Similarly STODDART and RASMUSSEN (1947) have shown how observations on sheep grazing habits can help to increase the efficiency of management on American ranges. Thus as an appendage to a managemental investigation behaviour studies may often be invaluable, but as independent investigations it must be admitted that their immediate bearing on animal husbandry is at present limited.

THE FACTORS WHICH INFLUENCE FEEDING BEHAVIOUR

The results obtained from continuous periods of animal observation can explain the 'how', 'when', and 'where' of grazing, but there

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still remains the 'what' and 'why'. A discussion of the difficulties of evolving an accurate and generally applicable method of evaluating the quantitative intake of herbage by a grazing animal comes outside the terms of reference of this chapter. It is, however, appropriate to discuss the observations which have been made to determine the type of herbage which grazing animals prefer to select, for these all depend upon a detailed knowledge of the animals' feeding behaviour.

The importance of observations concerning the extent to which various plants are consumed by animals has long been appreciated. In 1748 Carolus LINNAEUS, the Swedish systematist, wrote in a letter to a friend:

'This summer I continued my investigations as to which plants are consumed by cattle, which are ignored, and which are avoided; this work, in my opinion, is of fundamental importance both for private owners of livestock and for animal husbandry as a whole.' Unfortunately, however, although a large number of palatability trials have been reported, the results of which indicate the plant preference orders chosen by grazing animals under a variety of conditions, the results are frequently confusing and contradictory. These results make it clear that the old notion that a degree of palatability was a characteristic of a plant in the same more or less absolute sense as its earliness, hardiness or persistency is mistaken. The derivation of the term palatability implies a near relationship to the sense of taste, but, as the word is normally used in human and animal dietetics, a considerably wider meaning is intended. The adjective 'palatable' may in fact be taken as the nutritional synonym of the word 'attractive', and the palatability of a food is the sum of the factors which together operate to determine whether, and to what degree, the food is attractive to an animal. The term is, of course, used relatively and this often ignored fact has undoubtedly led to confusion in its use.

It is important to remember that palatability is a function of the animal rather than the plant since it is the action of the animal in accepting or rejecting a food that assigns to it a degree of palatability. The condition of the plant can, and very often does, have a great influence upon the grazing animal's behaviour, but this is only one of a number of factors which includes all the varying conditions of the environment and the animal's metabolism. For example, of initial importance is the species of animal under consideration. It is a common experience that a goat makes an obviously different selection from a cow. Also in their study of the palatability of various grasses and clovers TIEMANN and MUELLER (1933) found that while *Festuca pratensis* was definitely unpalatable to cows and horses it was accepted readily by pigs and sheep, and while *Avena elatior* was the first choice of goats it was almost untouched by sheep, horses and cows. Differences in the plane of nutrition also have parallel differences in food selection,

and the law of substitution may be applied to dietary preferences. As the need for food increases, the self-imposed standards of palatability tend to sink and, in cases of great need, animals will readily consume material which is labelled 'unpalatable' in text-books, and even that which is completely indigestible and even poisonous. Again, as every stockman knows, the individuality of an animal is a factor of very considerable importance and simple genetical differences in taste sensitivity within an animal species have been demonstrated experimentally.

Another extremely important fact which is within the experience of everybody is that the same plant species grown in different environments may produce different taste sensations. The possible reasons for this are again many. Some workers have stressed the importance of the level of the water table and the aspect of the land, others have stressed the climatic factor, and yet others have shown how the application of such artificial fertilizers as nitrogenous compounds, lime, bone meal, and various potash salts, all enhance palatability. The deposition of dung on the other hand gives rise to the growth of clumps which are avoided by almost all classes of stock. The work of GIOBEL and NILSSON (1933) has shown that if the clumps are cut and fed indoors to animals they are eaten with avidity and that the reason for their rejection in the field is the associated smell of faeces. That further variations in the palatability of an individual plant are caused by time as well as space differences is yet another important consideration. That the stage and rate of growth of grasses and clovers frequently have a critical influence on their palatability is an observation which requires no emphasis.

Exactly how such a wide variety of factors as this influences palatability is not known. It must be assumed, however, that they result in changes in the chemical and physical composition of a plant and that these changes correspondingly influence an animal's reaction to one or other of its sensory stimuli. The ultimate explanation of many grazing behaviour problems must await a more complete understanding of the special sensory mechanisms of the grazing animals and it is particularly unfortunate that at the moment our knowledge of this subject is extremely limited.

The general importance of the sense of taste in feeding habits is well-recognized and it has been suggested by RICHTER, HOLT and BARELARE (1938) that it has a special fundamental importance in food selection since through the blood system the reactions of the taste-buds may be related to the physico-chemical changes throughout the entire body. This suggestion has never been experimentally substantiated, and the little evidence that there is tends to refute it. Moreover, our present knowledge of the factors which determine the composition of ruminant blood makes it seem most unlikely that such a

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mechanism ever exists. The threshold values in the case of grazing animals for the four primary taste sensations have never been established.

If taste is the final discriminating mechanism in the choice of food the other special senses are undoubtedly of importance in the preliminary stages of discovery and selection. It has been suggested that smell is of very considerable importance in influencing the herbage selection of grazing animals. The only experimental evidence that is available, however (TRIBE, 1950b), shows that the value of the sense of smell is limited, and that olfaction can only be of supplementary importance in influencing the food selection of grazing sheep.

It is well-known that if an animal is kept in an atmosphere of a particular smell for a long enough period of time, its power to perceive that smell is rapidly lost, although the power to detect any other smell remains unimpaired. The grazing sheep lives always in an atmosphere saturated by the odour of, say, perennial ryegrass and white clover, or gorse and heather, therefore it is reasonable to assume that it can smell anything *except* those plants. If the animal comes into contact with an area of scented exotic species or an area contaminated with excreta, olfactory sensations will immediately be received and the animal's behaviour will depend on whether these are favourable or otherwise; of course, if the animal is in a situation in which the herbage is widely contaminated with, say, excreta then olfactory adaptation sets in for the smell of excreta and the plants in the area may be eaten readily.

The importance of visual stimuli must be considered from the separate standpoints of firstly the perception of form and distance, and secondly the perception of colour. From observation it is clear that the perception of form and distance is of assistance in the discovery of food areas, but its importance in the intimate selection of a particular plant, or part of a plant, is undoubtedly limited. Since it has been reported that sheep failed to associate a red or blue colour with the palatability of their food during the course of an experiment designed to test for colour vision (TRIBE and GORDON, 1950) it may be concluded that sheep are colour blind. Although it remains to be confirmed experimentally it seems probable that the vision of other grazing animals is similarly limited.

Our appreciation of the part played by the sense of touch in the selection of herbage is even less than our appreciation of the part played by the other senses. One of the reasons for this is that the tactile sense is extremely difficult to investigate experimentally. It is impossible, for example, to destroy it by obliterating the associated nervous tissue since the nerve which transmits tactile sensations is a mixed nerve and its destruction would interfere with other activities of the buccal region. There are some obvious cases of plants being rejected by grazing animals on account of some gross structure which can easily be related to an unfavourable sensory impression or even to

digestive discomfort. For example, the observations of LINNAEUS himself (1749) show that the very hairy or woolly plants, *e.g.* the *Verbascum* species, are almost invariably rejected by sheep. Again Linnaeus has recorded that such plants as *Pinguicula alpina*, which have an especially greasy texture, are also rejected. These gross structural abnormalities, however, are the exception and it is the finer macroscopical, and even microscopical features which are commonly of greater significance. Presumably such factors as particle size, water content, fat content, surface shape and hairiness all have some bearing on the subject but nothing except generalizations and a passing mention of the possibilities involved can be made at this stage.

It is often assumed that one of the more important factors which decides whether, and to what degree, food is selected by animals, grazing and otherwise, is the nutritive value of the food itself. In 1923 TSCHERKES observed that fowls suffering from polyneuritis sought only green food and refused to accept grain, and this he described as a 'triumph of instinct'. More recently Sir George STAPLEDON (1948), when discussing the nutritional wisdom of farm animals, has assumed that 'the animal has an instinctive drive to endeavour to satisfy all its nutritional needs'.

This subject is of importance for two reasons. Firstly, there are obvious economic advantages in a 'cafeteria' system of feeding for fattening cattle, pigs and poultry which are housed indoors. Secondly, grazing animals are inevitably on a self-selection system of feeding and if they do possess an infallible appetite instinct then it follows that the behaviour of a grazing animal is a legitimate criterion of the nutritional status of the pasture on which it grazes. Translated into practice this means that when animals are observed, as they often are, eating weeds, and perhaps bushes, when enclosed on a highly productive modern ley, it is right to conclude that they are following the dictates of their instinct and that there is some essential nutrient in the weeds that is missing from the sown herbage. Therefore, it follows that farmers should plant weeds, or herb strips, in their fields and so satisfy the nutritional requirements of the grazing animals. Since the production of total digestible nutrients from weeds is very much lower than from the same area of modern strains of grasses and clovers, this question has a very considerable bearing on the total yield of animal products from a unit area of grassland, and such a system must clearly have experimental verification before it can expect general recognition.

As HARRIS and his associates (1933) at Cambridge have pointed out, it is very unsatisfactory to let this matter be ascribed vaguely to some unexplained 'instinct'. Are animals in fact able to select their own diets according to their individual nutritional needs? If so, what are the limitations to such powers of recognition, and what is the mechanism involved? Many workers have interested themselves in

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the answer to these questions and much work has been reported on a variety of animal species under a variety of conditions.

Most of the experiments with farm animals have been conducted indoors where cattle, pigs, sheep or poultry have been allowed free access to a number of common feeding-stuffs which, if mixed together according to nutritional theory, are known to permit normal growth and function. In general it seems that whereas the food preferences of pigs and poultry often vary with their degree of development and reflect in general terms the animal's physiological need, the choice of calves, heifers and sheep certainly cannot be relied upon to produce normal, healthy animals. Recently, for example, GORDON and TRIBE (1951), studied the feeding behaviour of some pregnant Cheviot ewes kept on a self-selection system of feeding. The ewes, all bearing twins, were housed in individual pens and given the choice of a protein concentrate, a carbohydrate concentrate, hay, minerals and water. The amount of food eaten by each ewe voluntarily decreased throughout pregnancy and all but one ewe failed to select a ration that allowed them to bear and rear healthy lambs. Although the results of some of these self-selection experiments are contradictory and it would consequently be unwise to draw wide conclusions from them it does seem certain that the feeding behaviour of farm animals is not an infallible guide to their nutritional requirements.

Similarly a great many dietary self-selection experiments have been carried out with rats, and the results obtained from these reflect the same kind of disagreement shown by experiments with other species. It is usual to confront the rats with a wide choice of all the necessary basic foodstuffs, in solid and liquid form, in a so-called 'cafeteria' system of feeding. With such a system as this some observers have found that rats select a diet which closely agrees with that prescribed by nutritional theory, and under those conditions the animals grow and reproduce at a rate comparable to that of rats fed well balanced laboratory stock diets. Other investigators, however, have been unable to reproduce these results and indeed some have failed to demonstrate any ability on the part of the rat to select an adequate diet when fed on a free choice system. Similarly studies carried out on rats deficient in certain specific nutrients have in some instances demonstrated a correct selection of the missing item and in other instances the rats have consistently refused to eat the necessary nutrient and have thus committed virtual suicide. For instance RICHTER and HAWKES (1940-1) reported that rats deprived of various components of the vitamin B complex developed a craving for these vitamins, while WILDER (1937) found that a tendency to select an unfamiliar diet counteracted the selection of an antirachitic diet by rats previously subjected to a rachitogenic diet. The rats selected the novel food whether or not it corrected their deficiency.

SCOTT (1946 *et seq.*), working at the University of Pittsburg, has done a series of very carefully controlled experiments on the self-selection of diet by rats. He has found the same as other workers that sometimes a rat chooses a good diet and sometimes a bad, and has classified appetites under three headings; true hunger, trivial preferences and learned appetites. The desire for food as such is the only true hunger. Trivial preferences are most familiar in everyday life and include preferences for a pleasant taste, a satisfying smell, or an attractive texture, which are not directly related to nutritive value. Learned appetites include that of the vitamin B complex deficient rat for a diet containing vitamin B. As Harris concluded from his original observations the apparent nutritional wisdom of animals is not due to an inherited instinct for the right food but rather to a previous experience of the beneficial results which follow its consumption. In place of 'a little of what you fancy does you good' one might write 'you get to fancy a little of what does you good promptly'.

From a great deal of experimental evidence of this nature it is now clear that sometimes an animal selects what is best suited to satisfy its requirements and sometimes it does not. The mechanism which enables an animal under certain circumstances to select an adequate diet is not fully understood and this remains a problem to be solved by future physiological research. The answers to our husbandry questions, however, are clear. Since feeding behaviour is not an infallible guide to nutritional requirements it would be unwise to base a system of animal grassland management on the recorded observations of grazing animal behaviour. The limited amount of work that has been reported with grazing animals confirms this conclusion. It has been shown, for instance, that there is no relationship between a grazing animal's choice of food and the sugar, protein, mineral or vitamin contents of that food. There are some cases when grazing animals apparently exhibit 'nutritional wisdom' as, for instance, when cobalt deficient sheep show a preference for grazing areas which have been treated with cobalt fertilizers, or when phosphorus deficient cattle eat bones. Perhaps in some of these cases the animals are responding to specific nutritional factors, although that has never been proved, but in the two examples mentioned investigations have shown that it is incorrect to ascribe such behaviour to 'nutritional wisdom'. STEWART (1953) investigated the behaviour of cobalt deficient sheep in Scotland and concluded that it was not a craving for cobalt that stimulated the deficient sheep to graze strips of grassland which had been cobalt treated. He was unable, however, to show by differences in the botanical or chemical composition of the dressed and undressed pastures what the real reason was for such behaviour. The behaviour of phosphorus deficient cattle was studied in the Isle of Skye and although the experimental animals showed grossly perverted appetites,

osteophagia and allotriophagia being common features, the perversions were of a non-specific nature and no particular craving for phosphates *per se* could be demonstrated. Also the only critical experiment yet conducted on the subject (TRIBE, GORDON and GIMINGHAM, 1952) indicates that although cattle often show a preference for 'weeds' and coarse herbage when grazing a productive ley consisting of stimulated herbage of only a few selected species and all at a comparable stage of maturity, there is no reason to suppose that they benefit by eating them. It has been postulated that grazing animals often show a partiality for weeds because such plants generally have a high mineral content, and some people have even suggested that the absence of weeds may lead to deficiency diseases in the animals grazing them. It is well-known that under certain conditions (see Chapter 4) mineral and trace element deficiencies do occur in grazing animals but those are the exception, and, in any case, they cannot be cured by merely offering the animals a wider range of vegetation. That such deficiencies are unlikely to occur under normal ley conditions has been emphasized by BLAXTER (1952). He has calculated the approximate minimal requirements of minerals, trace elements and vitamins for herbivora, pigs and poultry, and, by comparing these figures with numerous published results of herbage analyses, he has been able to show that it is most unlikely that animals grazing normal pastures or leys will ever be receiving a diet deficient in minerals or trace elements.

Since the study of animal behaviour is a novel departure for agriculturalists it is important that the object of such studies should be properly understood. Those whose main interest is an *immediate* increase in animal production are better advised to follow other lines of enquiry since their activity in the fields of behaviour frequently only serves to confuse the issue for their colleagues, and such work will certainly not lead to any quick or revolutionary method of improving the efficiency of animal production. The argument which some are inclined to advance that the desire to study animal behaviour for its own sake and without continuous reference to husbandry is 'merely academic and should, therefore, be avoided' is misleading. The history of scientific investigation teems with examples of the reciprocity of interests between the fundamental and the applied. In various fields of enquiry it has been shown that not only does the elucidation of abstract principles open up new pathways for practice, but, conversely, that the minutest details of practice provide a stimulus for thought and a challenge to experiment without which 'thought languishes in the empty framework of its own categories, and experiment, lacking a fulcrum, fails to secure sufficient leverage'. If studies of the behaviour of farm animals are to be of value then we must begin by ensuring that their principles are rationalized and their techniques are specialized. Most important of all, the present tendency of basing systems of

animal and pasture management merely upon behaviour observations, or of using behaviour observations as the sole criterion of good management, must be exposed as irresponsible lest the damage this does to the general reputation of behaviour investigations should embarrass the more legitimate studies in this field. It nevertheless remains true that the essential criterion for comparing the efficiency of different systems of grassland or animal management must be animal production, and for a complete and critical appreciation of production records a detailed knowledge of the behaviour of the grazing animal is essential.

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CHAPTER 13

SEXUAL BEHAVIOUR

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BEHAVIOUR patterns can be classified according to the extent to which the animal's movements or actions are determined by the environment or are 'innate'. In the lowest class may be placed those activities which involve the least integrated co-operation of brain, nerve, and muscle and are almost entirely determined by forces external to the animal, for example, the aggregation or dispersal of animals by currents of air or water and by gravity or surface tension. In such cases the part played by the animal may be entirely passive, though the pattern of behaviour may be affected by the structure and composition of the animal's body or by the random movements which the animal makes. At the other end of the scale are those patterns of behaviour which appear to be almost independent of the environment; they appear to be 'ready made', 'endogenous' or 'instinctive'. In discussing this class of behaviour, the environment is not often entirely ignored but many writers regarded it as of quite secondary importance; as if offering an obstacle to be overcome by the 'instinctive drive' or as giving an opportunity for its expression. In using such terms as 'instinctive', 'innate', or 'endogenous', we risk the charge of using subjective or esoteric conceptions and it is important to keep in mind that although behaviour patterns can be relatively free from immediate environmental determination, it is only the obscurity and complexity of the action which causes us to miss the material connections between the environment and the behaviour pattern which is initiated. There is less risk of esoteric or dualistic conceptions obscuring the analysis of those behaviour patterns which we term taxes, kineses, and reflexes as by definition these are to be traced back to material cause or stimulus, even though the causal chain may be quite as obscure as in the case of an 'instinct'.

This preliminary discussion is particularly appropriate to the subject of sexual behaviour because in the literature the terms 'sexual instinct', 'urge', 'drive', 'libido' *etc.*, are frequently misused as if denoting esoteric forces and as the 'cause' of the behaviour under discussion. This is unfortunate because sexual behaviour has in fact been studied quite objectively in relation to underlying physiological functions of the sexual organs, the nervous system and the endocrine

system. It is the aim of this Chapter to show how sexual behaviour patterns can be described and understood in terms of accepted physiological principles.

THE EFFECT OF ANATOMICAL STRUCTURE ON SEXUAL BEHAVIOUR

Sexual behaviour patterns are in very large measure determined by the anatomical structure of the animal. It is easily understood that the whale, the giraffe, the monkey, the sheep and the mouse must exhibit quite different patterns of courtship and mating, and that these differences will be to some extent related to the sizes and shapes of the different species mentioned. Much less obvious differences than those distinguishing the species mentioned may play quite significant parts in determining characteristic behaviour patterns. As illustrating this a parallel may be drawn between the sexual anatomy of the horse and bull, and their characteristic mating behaviours. The stallion differs from the bull in having a typical vascular penis in marked contrast to the fibro-elastic penis of the latter animal. In the non-erect condition the horse's penis is quite flaccid and is with-

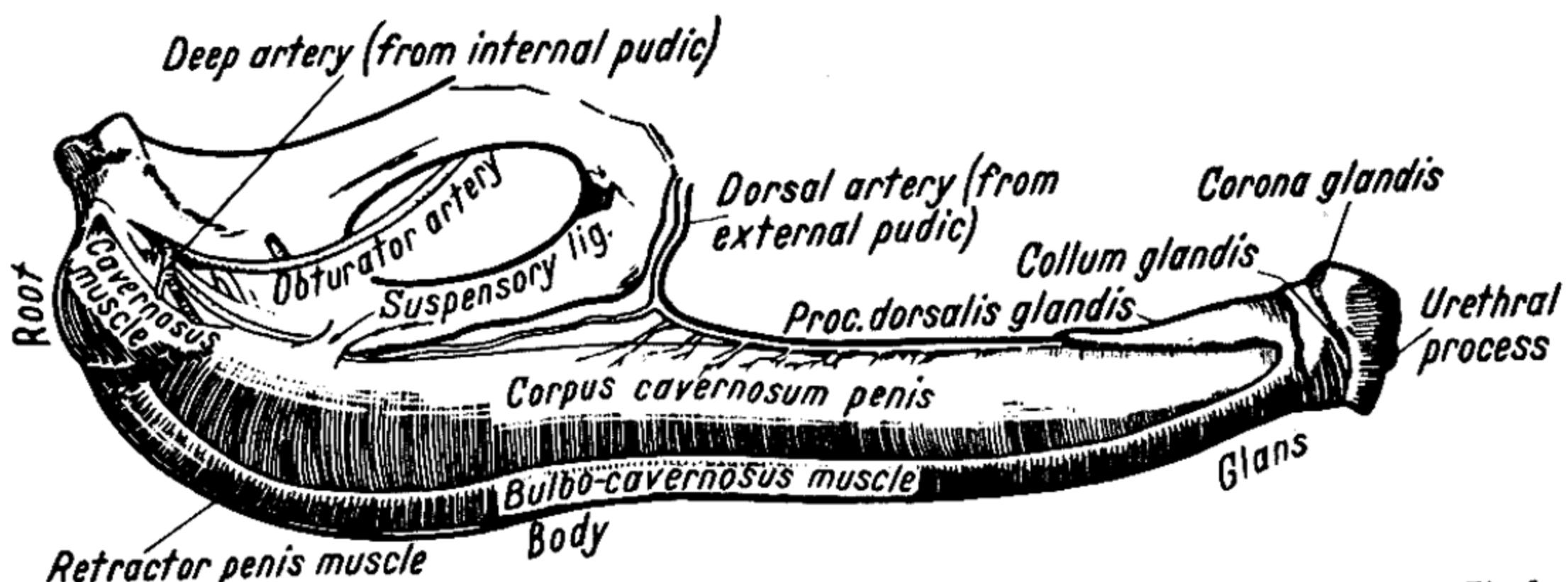


Figure 13.1. Penis of horse: lateral view. (Sisson Crossman (1945) by courtesy W. B. Saunders.)

drawn within the confines of the prepuce. The retractor penis muscle is relatively undeveloped and adherent to the ventral surface of the penis. There is no sigmoid flexure (Figure 13.1). Erection and pro-trusion of the penis are affected by gradually increasing tumescence of the erectile vascular tissue in the corpus cavernosum penis. Erection usually takes place rather slowly, and depends upon the continued reception of erotic stimuli derived from courtship and foreplay. Foreplay appears to be an essential accompaniment of vascular erection and this is well featured in the behaviour pattern of the stallion.

By contrast with the stallion the bull exhibits little or no foreplay prior to mounting and copulation. The penis of the bull is of the fibro-elastic type. It is of small diameter and relatively rigid even in the non-erect condition. The erectile tissue is small and the penis undergoes little enlargement on erection although it becomes more

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rigid. Protrusion is affected partly by erection but mostly by relaxation of the retractor muscle and by straightening of the sigmoid flexure (Figure 13.2). In mating with the cow there is little or no foreplay. The bull 'tests' the cow by smelling or exploring the vulva with muzzle or tongue and by placing the chin on the cow's tail head. If the cow is not on heat, she moves away rapidly and evades the bull's attempt to mount, if she is on heat she stands still and accepts service, which is performed with great rapidity. This example should suffice to illustrate the importance of anatomical structure in determining behaviour. A more exhaustive comparison of sexual behaviour patterns has been given in a previous paper (WALTON, 1952) in which the comparison is extended to cover smaller differences in the sexual tract, such as differences in the structure and secretions of the accessory glands.

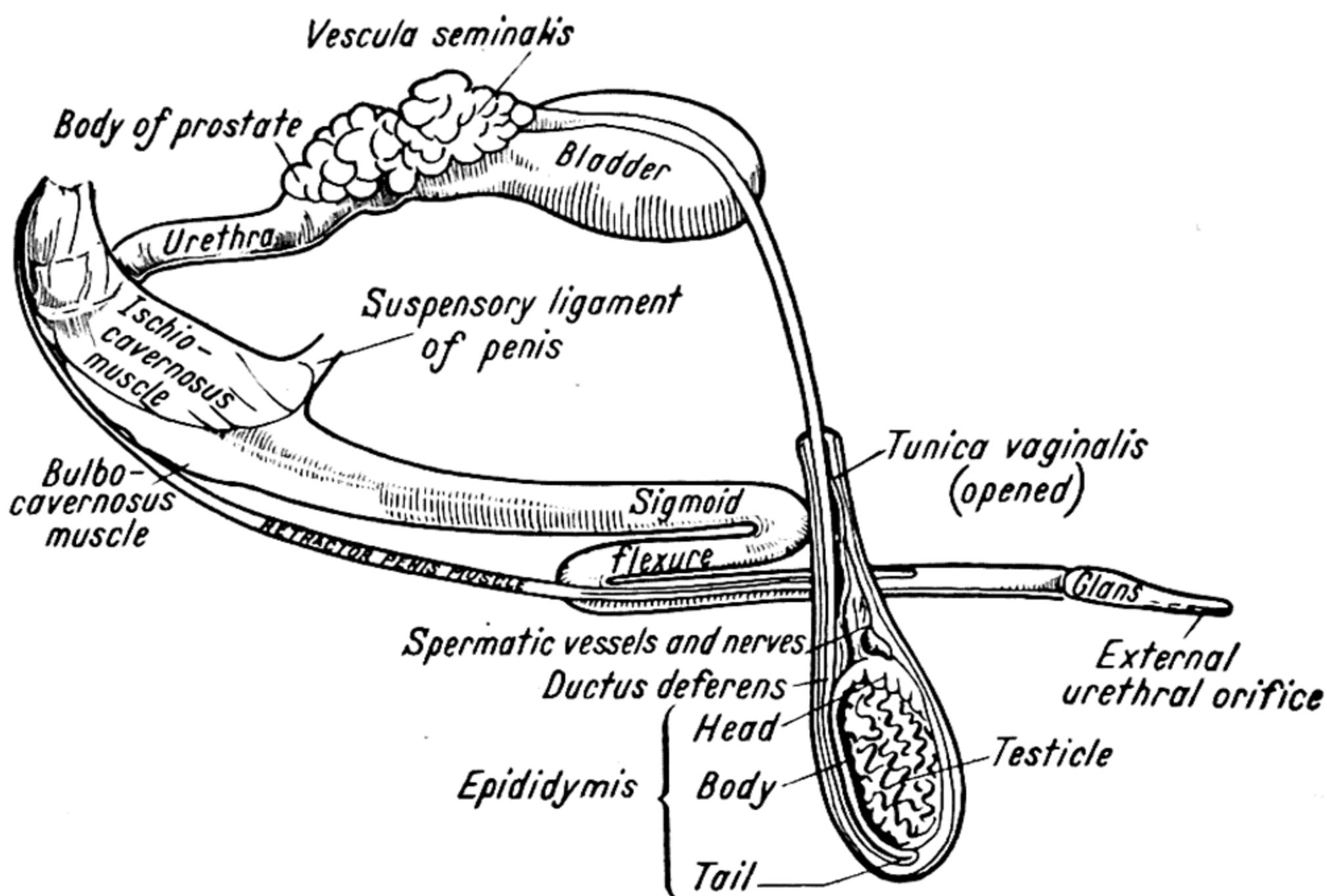


Figure 13.2. General view of genital organs of bull. (Sisson Crossman (1945) by courtesy W. B. Saunders.)

Where the complete pattern of bisexual copulation is considered, the structure of both the male and female sex organs, and their relationship to each other, may all profoundly affect the behaviour pattern. For example, the intromission of the penis, or the deposition of the vaginal plug alters very much the motor behaviour of the female rat during coitus.

BEACH (1952) has studied the relationship between anatomical structure and behaviour by a different and more experimental approach. In attempting to find an answer to the question how hormones affect behaviour, he showed that in the rat early removal of testosterone by castration at birth interfered with ability to copulate later in life, even when testosterone in sufficient quantity to restore

libido was then administered. This result was attributable to interference at an early critical stage with the normal growth of the penis, which failed to reach a size adequate for intromission and subsequent ejaculation. In further support of this hypothesis it was shown that a very similar pattern of sexual behaviour was in fact shown by non-castrated rats with surgical shortening of the os penis. BEACH (1952) also showed that castration has a very marked effect upon the cornified papillae in the integument of the glans penis of the male rat. This reduces the tactile sensitivity of the penis and interferes with the ejaculatory responses (BEACH and LEVINSON, 1950). Thus although castration was the primary cause of the change in behaviour pattern the immediate cause was the alterations in structure of the penile integument.

In both of Beach's examples, dependence of the sexual function upon anatomical structure was demonstrated by surgical mutilations or by interference with the normal endocrine status. Such experiments do not always give unequivocal results, since mutilation and interference often produce complications which obscure the direct issue. Nevertheless we can accept as a generalization, that as the anatomical conformation of the animal and the pattern of behaviour which the animal follows in the performance of mating are closely related, mutilation of the former will, with high probability, be followed by impairment of the latter. This generalization must also hold when mutilation or interference with function results from pathological causes.

THE EFFECTS OF THE NERVOUS SYSTEM ON SEXUAL BEHAVIOUR

There is an extensive literature on the part played by the brain on sexual behaviour which is derived from studying the effects of experimental brain injury. BEACH (1942) summarizes early work as follows: 'In the interpretation of effect of brain injury it is usually recognized that post-operative loss of a reaction constitutes only presumptive evidence as to the function of the neural tissue removed. The fact that a given response cannot be elicited after the destruction of a particular area in the brain is not conclusive proof that pre-operatively the missing area mediated the response in question. The converse of this principle is equally important. Post-operative survival of a response is not proof that the tissue destroyed originally had no function in the mediation of that response. Although a spinal dog or cat may show penile erection, ejaculation and certain postural adjustments characteristic of copulation, and despite the fact that the male frog may maintain sexual amplexus after decapitation, and, even though a state of satyriasis is often observed in hanged criminals, we cannot agree with one outstanding neurophysiologist who passes from such evidence to the following conclusion: "It is clear, therefore,

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that the patterns of sexual behaviour are laid down in the spinal cord". Despite frequent post-operative survival of copulatory behaviour it appears unsafe to assume that sexual excitability is unaffected by brain injury'.

As a result of his own experimentation with rats Beach has shown that even extensive cerebral decortication has little effect upon the female's response to the male, but in males the percentage which continue to copulate after operations, is inversely related to the percentage of cortex removed (Beach, 1940, 1952). When decorticated males do copulate, their behaviour reveals no obvious interference with the normal sensory or motor elements, but the operation does appear to affect the responsiveness of the male to the receptive female. The results from other animals are not identical or entirely confirmatory, but Beach (1942) concludes that although there is no evidence to suggest that a 'sexual centre' exists in the brain, the male's susceptibility to sexual arousal is in part a function of forebrain activity and the forebrain may be the location for a 'central excitatory mechanism', itself excitable and co-ordinating sensory impulses from receptor systems and mediating motor responses towards a definite pattern of behaviour. While therefore there is little to suggest from experiments on brain injury that any adequate explanation of sexual behaviour in terms of brain function can be given, an objective approach to the problem has at least been made on neuro-physiological lines.

Some experimental, but somewhat empirical work on the nervous control of sexual behaviour has been carried out with the practical objective of obtaining semen samples by electrical stimulation. BATTELLI (1922) in an attempt to stimulate hypothetical centres for ejaculation in the medulla oblongata was the first to discover that in the guinea-pig an ejaculation of semen could be obtained by the passage of an alternating current of about 30 V between an electrode placed in the mouth and one inserted beneath the skin of the nape of the neck. MOORE and GALLAGHER (1930) independently describe this method and they used it to assay testis hormone activity by its effect upon the ejaculate.

The method is extremely drastic and throws the animal into muscular convulsions, owing to the simultaneous stimulation of all nervous pathways in the medulla oblongata, including sensory, motor and autonomic systems. Owing to the intensity of the reaction the method is inapplicable to animals larger than the guinea-pig. GUNN (1936), and GUNN, SANDERS and GRAINGER (1942), however, devised a method by which semen could be obtained from the ram by electrical stimulation without causing too severe muscular convulsions (*Figure 13.3*). In this case an attempt was made to locate centres in or near the spinal column rather than in the medulla. One electrode consisting of a stout copper wire insulated except at the tip was passed into the

rectum, a distance of about ten inches. The other electrode, a stout surgical needle, was inserted into the longissimus dorsi muscle in the lumbar region. An alternating current of about 30 volts from the mains, or from a battery from which the current passed through an interrupter and reverser, has also been used successfully to obtain semen. Short repeated applications of the current are made. By varying the position of the electrodes Gunn was able to differentiate between an ejaculatory centre and a centre for erection situated posteriorly. Gunn identified these centres with the autonomic system rather than with the central nervous system. By placing the electrodes nearer the hypothetical centres in the lumbar region and not in the neck across the medulla, a smaller amperage is required to affect response and there is less stimulation of sensory and motor nerves. Nevertheless the ram has to be secured on its side on a table with the limbs and head firmly held in extension, and the animal's

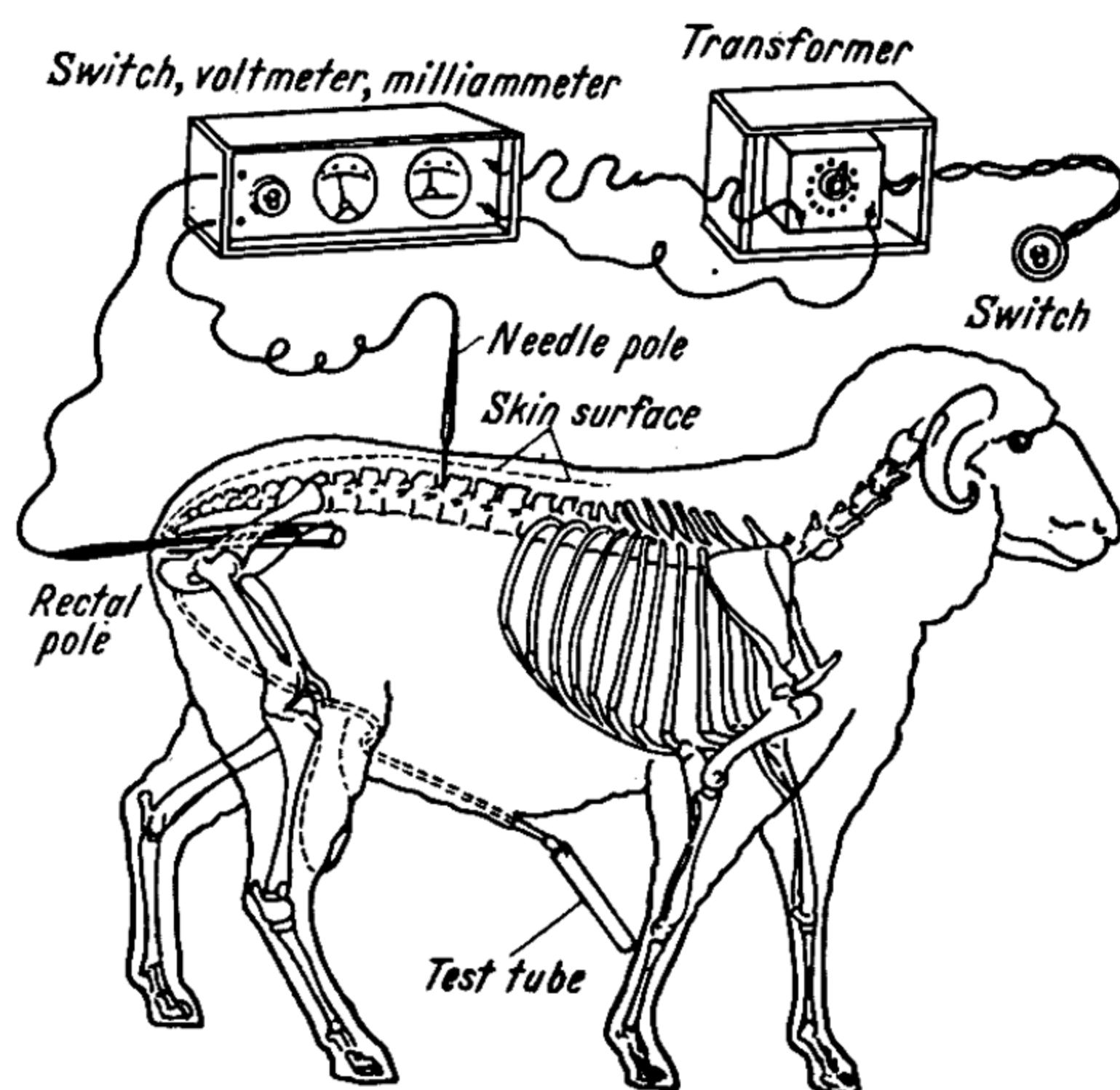


Figure 13.3. Diagram showing the method of collecting semen from the ram by means of electrical stimulation. (Gunn (1936) by courtesy Edward Arnold (Publishers) Ltd.)

reaction is violent and distressing if not actually hurtful. Gunn's method is not applicable to larger domesticated animals such as the bull or stallion.

The next advance was made by LAPLAUD and CASSOU (1945) who describe the use of a bipolar electrode inserted into the rectum. By eliminating the passage of excitatory currents across the spinal cord which caused strong sensory and motor reactions in the muscles of the hindquarters, they found that erection and ejaculation could be produced with very little distress to the animal. Not only could the

apparatus be used on the ram without restraint but it could safely be used on the bull and the stallion. The apparatus is more fully described by LAPLAUD, ORTAVANT and THIBAULT (1948) and by THIBAULT, LAPLAUD and ORTAVANT (1948). The original electrode was cylindrical, about 50 cm. long and 10 cm. diameter, and the terminals were 30 brass rings spaced about 1 cm. apart along the ebonite cylinder. The rings were connected alternately to the positive and negative poles of an alternating current passing through a sliding rheostat so that the strength of the current could be varied continuously by the operator. It was found that to get the best results the stimulating current should be applied gradually and rhythmically. At first a slowly increasing stimulation of submaximal strength is maintained for about 5 seconds and then reduced again to zero; after 10 seconds' rest the cycle is repeated and at each repetition the strength of the current slightly increased until the maximum is reached. The maximum is determined by noting the reaction of the animal. Usually after about 30 stimulations the animal postures as for copulation or masturbation, and the semen is discharged. LUTWAK-MANN and Rowson (1953) have shown that the first part of the emission contains no spermatozoa and is probably secretion from the urethral glands; then follows accessory gland secretions with increasing concentrations of spermatozoa. The sequence is the same as in normal coitus but is much more protracted, and usually much more semen is produced than in a single copulation.

A striking feature of the use of this method is that although there is little spinal stimulation of the sensory and motor nerves of the hind limbs, the animal assumes the postures and even makes pelvic thrusts similar to those accompanying ejaculation in the copulating male. Modifications have been made in the design of the electrode. Rowson and MURDOCH (1954) have employed for use with the bull an electrode consisting of two copper rings which are placed on the fingers of a rubber-gloved hand and can be held in position in the rectum. By this means it has been found that the 'centre' for ejaculation is situated near the ampullae of the *vasa differentia*. A further important contribution to the improvement of the method has been made by MARDEN (1954). As in the latest model of electrode used by the French workers, in Marden's electrode the terminals run parallel to the main axis of the cylinder, but the much smaller cylinder (about 30 cm. long) is placed totally within the rectum, causing less discomfort to the animal. Marden finds that both erection and ejaculation can be produced regularly with the very minimum of motor reaction, by using an electric pulse of sine wave form, and reducing the frequency from the usual 50 cycles per second to about 25 c/s. With this modification quite low strengths, less than 5 V and 0.9 amps., can be used. It is clear that by using a low frequency the nerves of the central

nervous system are barely affected, but those of the autonomic supply are strongly stimulated. The apparatus has not yet been used specifically for the study of behaviour, but the results so far indicate that erection and ejaculation are separately mediated mainly through the autonomic system and that stimulation of these nerves, or nerve plexuses, can elicit definitely co-ordinated patterns of behaviour. Erection consists of increasing tumescence of the vascular erectile tissue of the penis and protrusion of the latter by relaxation of the retractor muscle. Ejaculation consists of rhythmical contractions of the vas deferens, of the accessory glands and of the urethra so co-ordinated as to produce expulsion of semen. Accompanying these reactions of the male tract are definite muscular movements of the pelvic region (possibly reflexes) and perhaps also intense nervous excitement of the animal which usually accompanies orgasm. A whole pattern of behaviour and not merely a simple reflex discharge can be obtained by stimulation applied on the ventral side of the spinal column. It would be wrong to assume, however, that the whole pattern can be elicited by stimulation of a unique nerve centre, in which a rigid innate pattern is located. We do not yet know what nerves are actually affected and how far the initiation of one response may lead to a chain of secondary effects. It should be noted that to elicit response the stimulus requires to be repeated rhythmically which in itself constitutes a 'pattern'.

REFLEXES OF COPULATION

A reflex has been defined as 'an innate relatively simple and stereotyped response, involving the central nervous system and occurring very shortly after the stimulus which evokes it. It specifically involves a part only of the organism, though the whole may be affected, and is usually a response to localized sensory stimuli' (THORPE, 1951). We can recognize many reflexes mediating sexual behaviour, and if we departed from the strict definition given above and included all reactions of the stimulus-response type involving the central nervous system, we would include many if not most of the components of sexual behaviour patterns. Many of the less well-defined reactions may indeed be reflexes, and further analysis will show that they do comply strictly with the definition above, but for the present we shall describe only a few of those reactions which appear to fall within the definition given above.

The penis of the male is sensitive to both temperature change and pressure. In the case of the bull the copulatory thrust is given as soon as the erect penis comes in contact with the warm moist surface of the vagina. To elicit this reflex, the interior surface of the artificial vagina must have a temperature which may be slightly higher than that of the body, but must not be more than about three degrees below.

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Pressure and possibly friction between the surface of the vagina and the penis may also be components of the effective stimulus but are not so important. In the case of the stallion, however, the reverse is true. The copulatory thrust reflex is elicited by the penis coming in contact with the vagina, as with the bull, but as can be shown by use of the artificial vagina, pressure on the penis is most important and critical, while temperature can be varied considerably. In the pig, pressure appears to be most important in eliciting the pelvic thrust. In order to maintain coition, which in the pig is protracted, the artificial vagina is provided with a bellows or other means of increasing the pressure rhythmically. Temperature can vary within wide limits. These species differences in sensitivity may be related to differences in anatomical structure.

In the female obvious copulatory reflexes come into operation when the oestrous female 'postures' on the near approach of the male or stands still on being mounted by the male, or when the penis is introduced into the vagina.

THE SENSORY RECEPTORS MEDIATING SEXUAL BEHAVIOUR

Courtship, foreplay and copulation are in most species intricate performances and it is very obvious that all the senses may be used to guide the mating pair to the culminating act of coitus. Impairment of the senses may therefore be expected to have a deleterious effect upon performance. Also when some reflex component of mating has become conditioned to a sensory perception, impairment of that sense may be expected to have at least temporarily a detrimental effect. It is, however, remarkable to what a small extent impairment or loss of the sensory receptors may affect performance. Copulation with receptive females still takes place when male rats have been deprived of the receptors of olfaction, vision, audition, tactile sensitivity in the snout, lips and vibrissae, and cutaneous sensitivity in the ventral portions of the body and scrotum (STONE, 1923; Beach, 1942). There is no one type of sensory receptor which is alone responsible for arousing sexual behaviour. Beach (1942) holds that there is, however, some indication that interference with any one of the senses reduces the ease with which sexual arousal occurs, and that elimination of two types of receptor may so reduce excitability that mating reactions are abolished. From this work on the rat, it seems probable that no single cue mediates sexual arousal but that a perceptual pattern of excitatory value may be derived from several features of the receptive female, such as characteristic movements in foreplay, lordosis, vibratory movements of the ears and perhaps other olfactory, gustatory and tactile cues.

Experience gained from the use of 'dummies' in the collection of semen from the domesticated animals, *e.g.* stallion, bull, ram, boar,

dog and rabbit indicates that in these species, the simplest one initiating sexual response in the excitable male is a model only roughly the size and shape of a female of the species, which remains stationary on approach of the male and can be mounted. If on mounting, the penis is directed to an artificial vagina, the male may complete the mating pattern with intromission, pelvic oscillations, copulatory thrust, and ejaculation. Even some young males which have not previously copulated with a female will respond to the dummy on first presentation. There is, however, great variation in the excitability of individual males. Some males will not respond to the dummy; some will respond only after training with an oestrous female in the same stance as that in which the dummy is later placed. In this latter case some sensory cues other than those provided by the dummy are themselves effective or they act as reinforcements. Since one of the functions of the dummy is to provide a mechanical support for the male in such a posture that an artificial vagina can be applied to the penis and elicit the thrust reflex and ejaculation, it is not clear how far the dummy does provide sensory cues or how far it provides simply a situation in which the mating behaviour pattern can be exhibited without inhibition or frustration. The occurrence of masturbation which is commonly observed in some males of all the domesticated animals, except possibly the rabbit, may indicate that initiation of sexual activity is not in fact entirely dependent upon sensory cues derived from a female or female-like object.

HORMONAL ASPECTS OF SEXUAL BEHAVIOUR

The hormonal aspects of sexual behaviour have been comprehensively studied and the voluminous literature very fully summarized by Beach (1948). Recent progress has also been discussed at the Ciba Colloquia on Endocrinology, 1952. There is no need to make extensive commentary here. Early conceptions of hormone action in relation to sex were relatively simple. In the male the testis secreted male hormone which was responsible for growth at puberty of the sexual organs, the accessory glands, the secondary sexual characters and of male behaviour. With the appropriate changes the same conceptions were applied to the female. These conceptions are now known to require considerable modification. Male and female behaviour patterns are not sex specific. Under certain conditions males may exhibit female behaviour and females exhibit male behaviour. Castration generally results in loss or impairment of sexual function but not always, and administration of male or female hormones may initiate or reinforce the appropriate behaviour pattern, but not invariably. The issues are further complicated by the parts played by the anterior pituitary and the adrenal cortex in the sexual syndrome. One of the main interests, however, in the relationship between hormone and

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behaviour centres round their mode of action. We have already referred to the part which hormones may play in changing the anatomical structure of the sexual organs (p. 20) or altering their sensitivity, but a direct effect upon the nervous system also appears to be accepted by most authorities. The evidence for this is not unequivocal but it is probably safe to postulate that a higher concentration of androgens in circulation will raise the excitability or lower the threshold of response of the male to a sexually excitatory object such as an oestrous female, and that there is a similar quantitative relationship between oestrogens and the female. The mode of action of the hormones on the nervous system is unknown.

A SYNTHESIS OF THE COMPONENTS OF SEXUAL BEHAVIOUR

In the preceding sections the approach has been entirely analytical. An attempt has been made to show what components can be singled out for separate consideration and a causal relationship established between the component and the underlying physiological function. It is necessary to show now how the components can be reassembled to give a coherent representation of behaviour of the whole animal.

The first step in this synthesis is based upon work on the rabbit which made use of the artificial vagina and the 'dummy' (MACIRONE and WALTON, 1938). It was found that males differed considerably in the responses they made to the dummy. Furthermore the responses made by any one male varied as the dummy was made more or less sexually exciting to the male or was replaced by an oestrous female. Thus two variables were observed; the excitability of the male and the excitatory value of the sexual object, female or dummy. 'In our experience', write Macirone and Walton, 'completion of the sexual pattern depends upon two factors; first the sexual drive shown by the male and secondly the suitability of the sexual object. These two factors are supplementary to each other in causing the completion of the sexual pattern. For example, a strong male requires only the minimum of suitability of the sexual object to produce ejaculation while a weak male may require the maximum of suitability (*i.e.*, the oestrous doe)'.

This relationship was also developed by Beach (1942) who expressed the degree of sexual arousal as the product of two independent variables, excitability of the male and excitatory value of the female or sexual object.

A further synthesis can be made by combining a third variable. In the rabbit the male pattern of behaviour follows a definite sequence: (1) exploration, (2) smelling, (3) jumping, (4) chin rubbing, (5) mounting, (6) gripping with the teeth, (7) pelvic oscillations, (8) exploratory movements of the erect penis, (9) intromission, (10) orgasm with ejaculation (Macirone and Walton, 1938). The three

variables are shown in *Figure 13.4* combined in a three dimensional representation. Increasing sex drive or excitability is plotted along the abscissa, and excitatory value as the ordinate in the plane of the paper. Rising vertically to meet at the apex of the pyramid (orgasm) are the persistency values marked by certain stages in the copulatory sequence. Two examples may help to make the diagram clear. A male with weak drive (1) will not react to an inanimate mount, nor with the animate mount, but will explore the dummy and will both explore and mount the oestrous female. A male with moderately strong drive (3) will explore an inanimate mount, mount an animate mount, and copulate and reach orgasm with the dummy and the oestrous female.

In the diagram the position of erection and ejaculation in the copulatory sequence are shown by arrows. The reason is that these responses do not fall into the same category as the motor components. The latter are all primarily enervated by the central nervous system

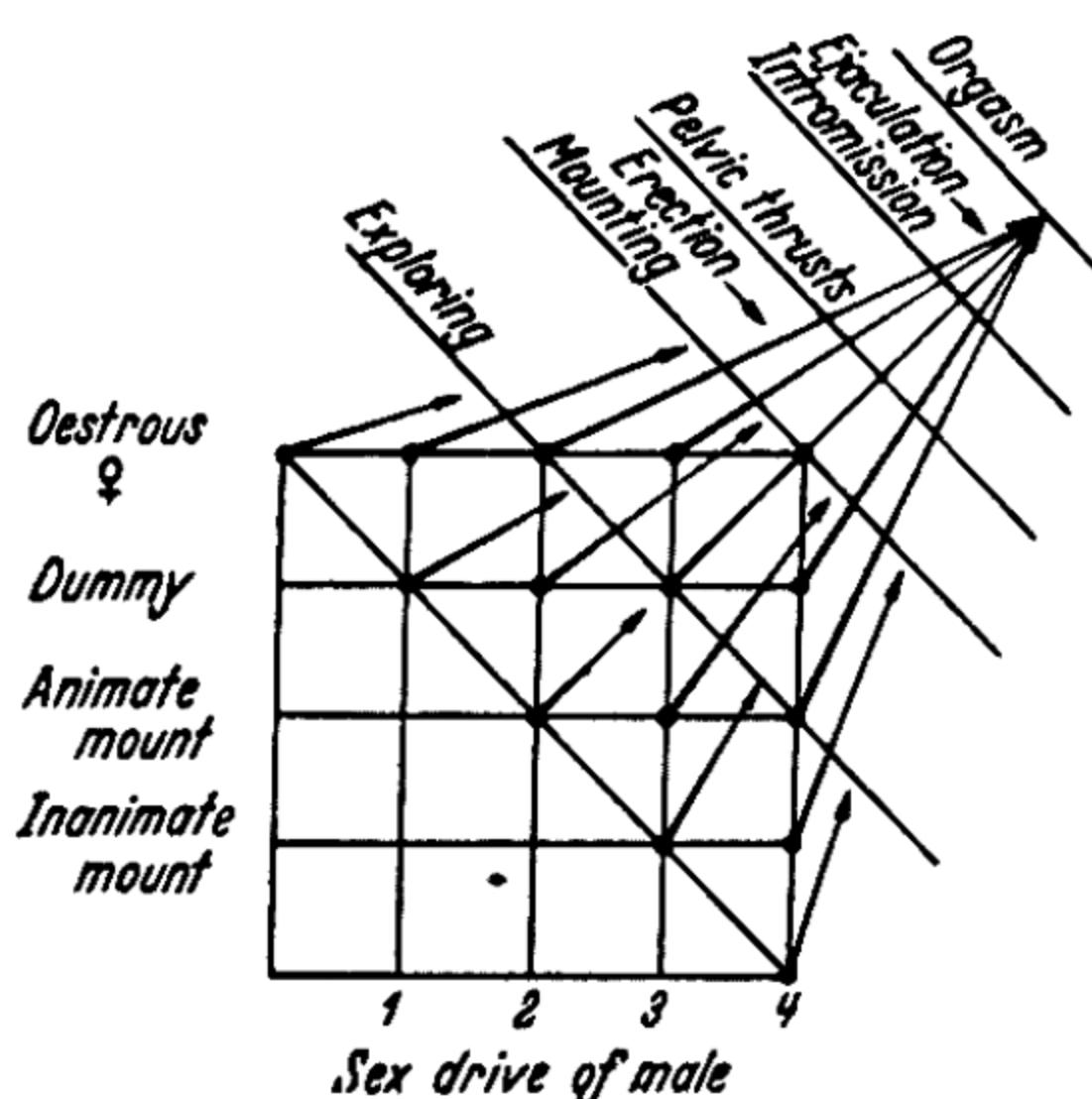


Figure 13.4. Sexual behaviour pattern in male rabbit (Walton (1952) by courtesy Proc. Soc. Study of Fertility).

and involve a high degree of cortical motor co-ordination. On the other hand erection and ejaculation, although they both involve muscular motor activity and cortical co-ordination are primarily enervated through autonomic pathways and can be made to function independently of the motor pattern. For example, delayed or incomplete erection is frequently observed in the stallion who may mount the mare before erection is complete, and premature ejaculation is a common sexual maladjustment in the human and is occasionally seen in young animals. The diagram can be used to represent other components of sexual behaviour. *Figure 13.5* represents its application to the relationship between sex drive as determined by abstinence or sexual output, and 'conditioning' which may be either in the direction

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of 'facilitation' or 'inhibition'. For further explanation and examples, the original paper should be consulted.

The study of animal behaviour and especially recent developments in ethology are in their infancy and there is much to be learned about 'instinct' and 'innate' behaviour. The domestic animals provide material which is easily accessible to the research worker, and it is

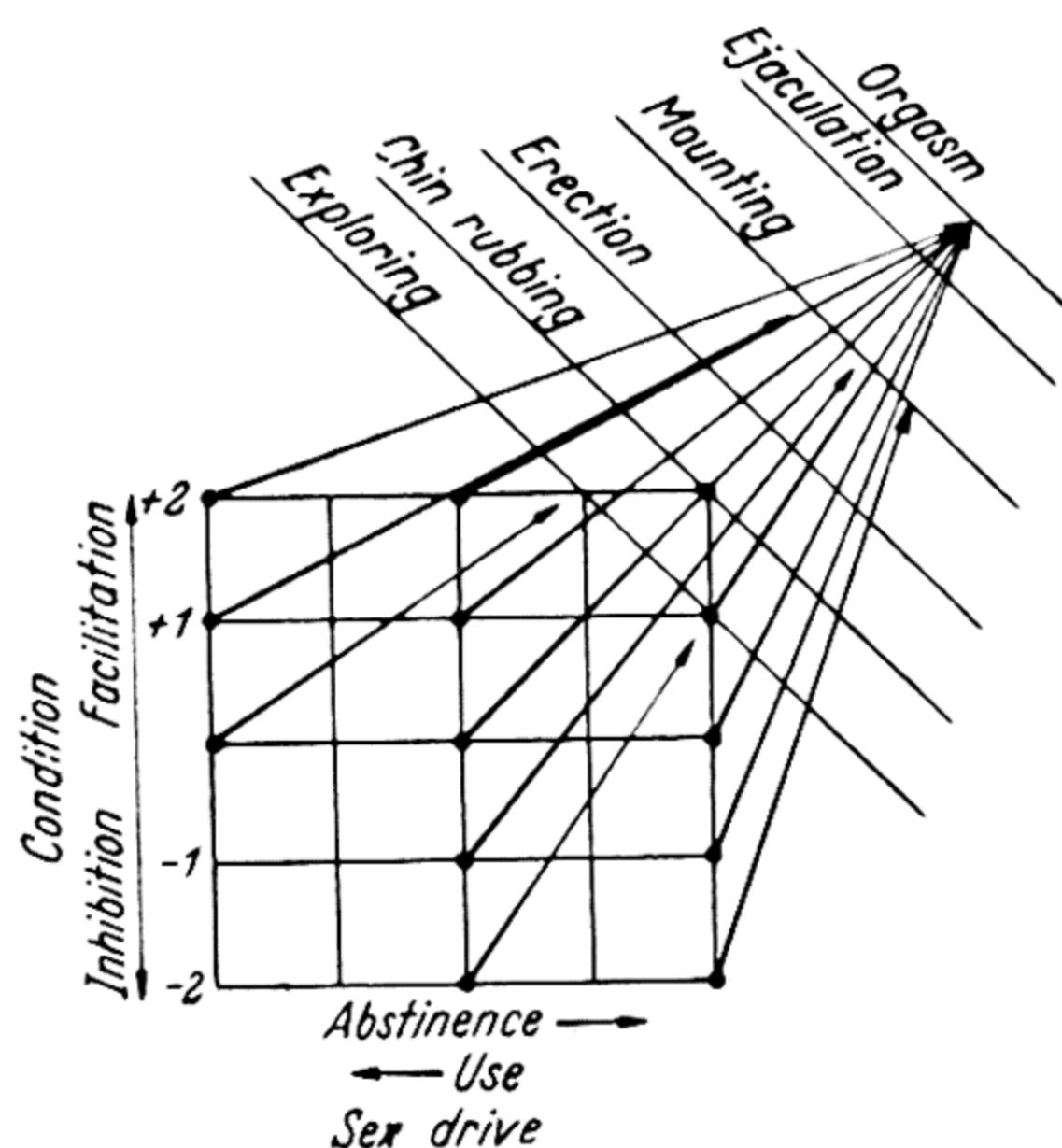


Figure 13.5. Sexual behaviour pattern of young bull (Walton (1952) by courtesy *Proc. Soc. Study of Fertility*).

probable that in the future domestic animals will be more used for the direct study of behaviour. In the present contribution the aim has been to link sexual behaviour with the underlying physiology, both by analysis of components and by resynthesis. This seems to be the approach most appropriate to this material since more is probably known about both behaviour and sexual physiology in domestic animals than in other mammals.

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LOCOMOTION

CHAPTER 14

THE MECHANISM OF MOVEMENT

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LOCOMOTION may be described as the act or power of moving from place to place—continuous progression from a state of rest. Motion may be described as a change from the state of equilibrium; the locomotory act is a deliberate and controlled change, the manner and duration of which determines the mode of progression. It is a vital body function, and the development of locomotory ability must be regarded as one of the most important factors in animal evolution. It requires the co-ordinated activity of many body systems or units, and to locomotion the state of these units at rest is as important as their state in motion. Correct posture is vital to itself and to the movement for which it is prepared.

Although it may rightly be said that interest in locomotion can be traced from the time when man seriously looked about him, it was not until the publication in 1680 of BORELLI's classical work *De Motu Animalium* that the study of animal locomotion was really placed on a scientific basis. Borelli may be described as a mechanist; it is known he was influenced by Galileo, and it is perhaps true that a mechanistic approach was necessary to place what was, and is, primarily a biological study on a scientific footing. But Borelli was by no means entirely mechanically minded in his approach, and he may too have been influenced by his contemporary Steno who wrote on the structure of muscles in relation to their function. However that may be, since Borelli's day the study of locomotion has engaged the attention of anatomists, physiologists, natural historians and mechanists alike. They were by no means isolated studies and each has gained from the other. It is, therefore, neither necessary nor desirable to classify them as being advances in any one division of science, but if classification is required one could instance—to mention but a few—in the field of anatomy and physiology the works of Hunter, Duchenne de Boulogne, Marey, Frederick Smith, Beevor, J. P. Hill, Sherrington, Mackenzie, Wood Jones and MacConaill; and in biomechanics Braune and Fischer, Weber Bros., Fick, Strasser, Elftman, Manter, Steindler, J. Gray and Howell.

Much of this work has dealt with the properties of tissues and has been directed primarily towards man, but man is not necessarily

peculiar in his utilization of units of the locomotory system, and the principles of locomotion are well illustrated by reference to comparative forms. Of the comparative species the horse has predominated as an example, indeed the form of modern *Equus* is representative of evolutionary trends whereby features necessary for speed and power have been retained as survival characteristics. The horse, then (although now less in evidence than hitherto due to the impact of a mechanical age), will be used for illustrating the principles of locomotion in farm animals with reference to other species only as necessary, on the assumption that the pattern is very similar and the differences which exist are for reasons which need little explanation or emphasis.

Of studies on the horse GOUBAUX and BARRIER (1892) have reviewed the anatomy in terms of the requirements of locomotion within a more generalized study of conformation, and F. SMITH (1912) has considered the movements of the limbs of the horse and the activators thereof. Smith has probably given the most lucid account of the part played by units of the limb during movement. He discusses, in anatomical terms, mobility of limb joints, integration of muscle activity, the propulsive effort of the limbs and the units responsible for support. Many other authors have written on features of horse locomotion to which later reference will be made.

GRAY (1944) has discussed the mechanics of the Tetrapod skeleton while considering the whole vertebrate body as a single mechanical system in which the function of individual muscles and bones is co-ordinated with those of all, or many of, the others. This approach is quite refreshing; although due regard must be paid to the activity of the part, it is essential ultimately to consider the whole body as a single functional unit. Such an approach allows also of common respect for form and function—in no sense can the two be divorced.

Of the many techniques applied to the study of locomotion few have been so valuable as that of the camera. From the early work of MAREY (1894) and the publication of *Animals in Motion* by Edward MUYBRIDGE in 1899—which book still remains the authoritative work on the gaits of animals—the use of the camera has gradually become an indispensable aid. It might be argued that it has not advanced the studies of animals in movement as portrayed by art—although surely it would have appealed to George Stubbs—that the artist requires a composite picture representing an impression, not exactitude or precise split-second detail. But so far as the student of locomotion is concerned, it has enabled him to study photographs and individual frames of ciné films taken at speeds varying from 16 frames per second upwards, and thus to record phases of motion invisible to the naked eye.

UNITS OF THE LOCOMOTORY SYSTEM

The units of the locomotory system are bones, joints, muscles, and their accessory connective tissues working under the control of the nervous system. In this regard it must be early emphasized, as has been stated by many workers, that it is a complete movement which is under the control of the will and is thus represented in the nervous system; in other words an animal does not will to move a particular muscle or muscles, it wills to move a particular part, great or small, of the body. It is customary for the anatomist to introduce units of this system in terms of structure at the same time indicating their function. It is also possible to review their salient features in terms of locomotory ability, and if support is required for this statement it will be found in the observations of those who have reviewed the evolution of animal locomotion. Among them is ZENKEVICH (1945), who leads the story through types of movement exhibited by minute and primitive forms to that of animals in possession of extremities. In the mammal the specialization of these extremities to a cursorial habit in such species as have adopted it, together with a more rigid body column, has led to greater refinements of these units.

Bone

Bone is the essential framework of the vertebrate body, the frame on which the other units of the system work. In this role bone is subjected to stresses and strains for which its architecture allows; indeed it is more possible to define the structure of bone in terms of mechanics than any other unit. As a consequence of these extrinsic forces a bone is capable of change both in external form and internal shape*. This is not to suggest that gross changes in bone structure are to be expected as the result of normal progression. On the other hand it is well known that exostoses of a pathological nature do occur on the limb bones, particularly of the horse, as a result of conditions of movement; and equally well known that they may be present to an alarming degree before they effect any noticeable change in the gait.

Classification of bones may also be regarded on a locomotory basis. The hollow long bones of the limbs are built for support yet are also economical in bone weight. The flat bones of the shoulder and hip allow of expansive surface areas for the attachment of muscles coming from all directions and, therefore, subscribe to a variety of action. The short bones of the carpus and tarsus markedly increase the mobility of these joints, and at the same time tend to diminish concussion by distributing thrusts resulting from impact with the ground. The irregular bones of the vertebral column are so named because of the numerous processes they possess, shaped to receive

* The need to consider bone as a living tissue has been stressed by LE GROS CLARK (1952).

muscles which by the so ordered direction of their fibres tend to bind the column, yet to allow of the necessary degree of movement for both progression and support. The position and nature of tuberosities, crests, and other projections of bone are obviously associated with the requirements of muscles, tendons or ligaments attaching thereto or passing thereover*. In similar light may be regarded the development of sesamoid bones in tendon.

Joints

Again, the nature of the articular surface of bones is related to movement, and in diarthrodial joints this also follows terminology, *e.g.* enarthrosis (ball and socket), ginglymus (hinge) joints. Much has been recorded by FICK (1921 and previously) and MACCONAILL (1946) on centres of movement of joints being dependent on growth of articular surfaces in all axes, for example modification to hinge from ball and socket action requires only slight changes in curve of bone. The cavity of a diarthrodial joint is completed by a synovial membrane which, in turn, is surrounded by a fibrous capsule. The fibres of the capsule are loosely arranged in interlacing fashion and as such allow of stretch and return. It would appear that the capsule functions chiefly to assist the synovial membrane in retaining synovial fluid. Not all diarthrodial joints have strong capsules such as the hip and shoulder, in which case ligaments, either extrinsic or the so-called 'thickenings of the capsule', and the close musculature of the joints, assist in retaining the joint fluid. The anatomical positioning of these structures is of clinical significance in that protrusions of synovial membranes occur at 'weak' anatomical spots, that is to say at places where there is a 'gap' between the retaining structure or where the capsule is particularly thin. Such is the nature of 'bog spavin' and 'articular windgalls' in domestic animals, common in the horse. Mention should be made also of capsular muscles attached to the capsule, as opposed to muscles passing in close proximity to a joint, and to synovial fat; the former, by no means universally present, are said to assist in tensing the capsule, the latter to buffer peri-synovial structures during movement.

Ligaments

As distinct from the capsule, the fibres of the true ligaments of a diarthrodial joint are more closely arranged and regular in distribution;

* It is doubtful if the mammal demonstrates an example of bone-muscle relationship so vital to movement as does the avian form. The two pectoral muscles of the bird have very similar attachments yet diametrically opposed actions, one depressing and the other elevating the wing. This is due to the tendon of one passing through an osseous foramen formed by the pectoral girdle which thus alters its line of action. Again in the bird, HECTOR (1894) has drawn attention to the presence about the elbow of the albatross of a sesamoid bone to which are attached fibres of the main extensor of the manus. According to Hector, when the wing is fully extended the thrust of this sesamoid causes a slight rotation of the ulna on the humerus thus locking the elbow joint, and this he gives as the reason for sustained extension during flight without muscle fatigue.

THE MECHANISM OF MOVEMENT

according to MACCONAILL (1937-38) many exhibit fibres arranged in spun style to allow of maximum stresses. It is interesting also to observe in a freshly dissected specimen twisting of entire ligaments such as is seen in the cruciate ligaments of the stifle of the horse when moved in flexion and extension. Ligaments have considerable influence on joint movement, although they have no active power and are in the main inextensible. Ligaments function to bind joints and they must also be regarded as structures which restrain and guide movements, for according to the plane in which they are set they will serve to guide the direction in which a muscle acts. Ligaments are present in several forms: as pronounced and aggregated thickenings of the capsule (*e.g.* many collateral ligaments), as interosseous ligaments (*e.g.* deep ligaments of the carpus and tarsus) or as being in direct continuity with the attachment of a muscle (*e.g.* the lateral musculature of the peroneal or fibular region). Within this last category may be included the straight ligaments of the patella, three in ungulates; but as tendons of insertion of the crural musculature of the femur on to the tibia, with mobile patella developed and interposed between muscle and tendon, they function as tendon as well as ligament. The so-called extension of the medial collateral ligament of the elbow and the suspensory ligament of the metacarpus/metatarsus in the horse are not true ligaments. The former represents the pronator teres muscle replaced by ligament, the latter the highly modified interosseous medius muscle of the third digit; in both cases here change in structure is related to change in function (*see* pages 625 and 637). An interesting subsidiary action is the stabilizing effect of collateral ligaments with excentric attachments relative to the centre of curvature of the joint; when the joint moves in a certain direction tension in the ligament is increased. A transitory maximum is of course reached beyond which point, or in the reverse direction, the ligament will relax potentially in spring fashion, hence the expression 'snap joints'. Such an arrangement exists in the elbow joint of the horse; in this instance maximum tension is not necessarily associated with a weight-bearing phase, and release-action would appear to aid flexion. A stabilizing or locking action of a somewhat different nature is noted in the stifle, again particularly in the horse (*see* pages 638, 639).

PARTRIDGE (1924) has suggested that ligaments and normal muscle tone are not sufficient to protect a movable joint from injury in ordinary circumstances, and has drawn attention to the close functional relationship which exists between the nerve supply to muscles crossing a joint and the joint itself. It is suggested that, when required, reflex action would initiate muscular contraction and thus aid in protecting a joint from injury. Even if not stimulated by a 'gentle' locomotory act, this potential represents an excellent example of the closely co-ordinated activity of structures effecting a movement.

Tendon

A tissue very closely resembling ligament in structure is tendon. Tendon, however, is part of the muscle unit, the non-contractile element, and its pronounced function in locomotion may be said to be directly complementary to that of the muscle fibre. Other than tendons of insertion, well-developed in the limb musculature, tendon is present at intersections of muscle fasciculi. This allows of the attachment of muscle fibres at varying angles to the long axis of the muscle; furthermore it allows of shorter muscle fibres than would be necessary were they required to run lengthwise and, therefore, of more fibres per given area. These tendinous intersections need not be connected to the main tendon of insertion; but in many instances they are, constituting variations of the penniform muscle fibre-tendon arrangement, in which case they may be regarded as extensions of the tendon of insertion into the muscle belly. If not connected to the main tendon there is a possibility of the muscle fasciculi with which they are associated competing with another similar group to effect actions in differing directions, but if connected the action of the muscle fasciculi is directed in the same overall direction. Further, this latter arrangement allows more fibres to be attached to the main tendon, and if the tendon within the muscle is multiple this facility is increased. Tendinous intersections can be regarded as attributes of strength as the power of a muscle is related to the number of fibres involved at any one time. In addition, they permit of muscle rest, either by allowing the less fatigable tendon to 'take the strain' or by allowing one part of the muscle to work while the other maintains tone.

Referring now particularly to tendons of insertion, it can be said they serve to 'order' the line of muscle pull and, in the limbs, the position of muscle bellies. It would be impossible, as many authors have pointed out, for large muscle bellies to be present about the extremities of a limb; nor is it mechanically desirable, particularly in species such as the farm animals, which exhibit little individual action of manus and pes joints. Since muscle bellies are situated in more proximal regions of the limbs their tendons are enabled to proceed without hindrance to the areas where the actual movement is required. HAINES (1932), when considering such problems as muscle traction and limitations of the range of possible contraction, has written on the laws of muscle and tendon growth. He discusses a basic architecture of a muscle-tendon complex and states that tendon length is related to muscle size in that the former can only increase at the expense of the latter—muscle fibre metamorphosis. This is a point of significance in comparative anatomy and can be related to the length of manus and pes and their contained tendons. Also well exemplified in comparative anatomy is the feature that if in the course of evolution a muscle loses the need to move a part it becomes replaced by tendon or

ligamentous tissue. Reference has already been made to this in the case of the pronator teres muscle of the horse, where with fusion of radius and ulna the act of pronation has become impossible and, therefore, muscle fibre redundant.

In conclusion it can be said that tendon is present as an aid both to movement and posture, and in the latter regard the more a muscle is used in support the more will be its relative content of tendon. The limbs of the horse, an animal which spends most of its life in the standing position, contain relatively more tendon fibre than those of the dog.

Muscle

ELFTMAN (1939 b), in a review of the function of muscles in locomotion, introduces the term 'tendon action' which he defines as transmission of energy by the muscle from origin to insertion. Elftman is discussing here the relation between energy received and work done, and he proceeds by stating that this transmission (tendon action) involves the presence of tension in the muscle, but neither reception nor expenditure of energy by the muscle tissue except for the production and maintenance of tension. This statement, although introducing a wider field of discussion in the article mentioned and applying the term 'tendon action' in a somewhat different sense than has been discussed above, may be used also to illustrate the functional unity between muscle and tendon fibre, that the two are constantly poised for action, and that the dominant element in movement is the muscle fibre. This predominance is due, of course, to the unique power of contractility exercised by the muscle fibre, the mode and analysis of which have engaged much research. It is not only a structural problem, it is a biochemical problem and relates to energy supply*. Muscle fibre is present in two forms, red and white, and both types may be found in the same muscle; the red fibre is said to be associated with postural requirements, the white with rapid movement. According to HAINES (1934-35) the length of muscle fibre is proportional to the possible range of approximation, and this statement cannot be divorced from consideration of the presence and arrangement of the tendon fibre. Again, size and shape of the whole muscle are dependent on the type of action required, and this, in turn, may be related to the arrangement of the locomotory unit or units with which it may be associated.

The simplest form of locomotory unit effecting a movement under control of the nervous system requires the presence of two bones, an interposed joint, a muscle to contract, and a muscle to antagonize in active relaxation. No muscle can act alone, but allowing for the necessary presence of an antagonist it must be rare even for any two

* For an appreciation of the biochemical aspects reference should be made to SZENT-GYÖRGYI (1947) and BALDWIN (1952), and for the more physiological aspects to DAVSON (1951).

muscles to act alone, in fact group activity is an established feature of muscle action. Movement about a single joint is usually the result of the combined effort of several muscles. Many muscles act on more than one joint, and their potential on the one may be directly opposite to their potential on the other. This is indicative of the difficulty encountered when endeavouring to estimate the part played by individual units in an analysis of whole limb or, indeed, of whole body movement. Relative to this it can be said that, according to circumstance: a pair or more of muscles will co-operate or antagonize, parts of the same muscle will act in different ways at different times—a factor dependent among other things on posture, and also—and a most important point—the action of a muscle in life may not be as its attachments suggest in the dissection room. Above all it must be realized that movement of an animal is dependent on established patterns controlled by the nervous system. In mammals these patterns can be varied according to circumstance, although, in the lower animals with less highly developed nervous systems, experiment has demonstrated that these patterns are fixed (*see WEISS, 1937, and others*).

When considering the combined activity of muscles and their ability to perform more than one action it might be queried how much an animal is dependent upon any one major muscle. In the course of an investigation made to determine what changes can be observed in the gait of an animal after the throwing out of action of one or a group of muscles, STEWART (1937) found generally it was not until three muscles in the limb of the rabbit were divided that noticeable changes could be detected. A similar observation has been recorded by LISHMAN (1908) following section of tendons in the limb of the horse. These experiments, and others which could be quoted, would seem to indicate that, provided the injury is not too severe and not at certain critical points, the animal can make immediate compensation: that there are other units capable of taking on the action of even major muscles. Support for this view may be found in clinical cases where it is difficult to arrive at a correct diagnosis, indeed even time may not reveal any appreciable change in the gait. Such problems form interesting functional anatomical studies.

As has been indicated, reference to the action of an individual muscle is dangerous, and in any case it is the whole movement, not the action of any of its component parts, which must be considered. Again, as has been said, it is difficult to assess the precise activity of any one muscle at a given time; nevertheless it is necessary to have a method of classification to which reference can be made. Such endeavours have engaged the attention of many authors; the most illuminating accounts are those by BEEVOR (1903), who summarizes the views of earlier workers, including John Hunter, by WOOD JONES (1944) and by

LOCKHART in Cunningham's 'Anatomy' (1943). That any method of classification is open to criticism may be associated with the danger of endeavouring to analyse group activities in terms of simple units. However, put in simplest form, any muscle which by its contraction effects the actual movement desired may be termed an agonist. Because, as judged from its attachments, it would be the muscle responsible for the observed movement and as such would be acting in prime capacity, it may be termed a prime mover. A muscle which directly opposes the prime action may be termed an antagonist; if the opposite action is desired the role of agonist and antagonist is reversed. A muscle which by its contraction assists the prime mover in some degree, often by controlling the plane of movement, may be termed a secondary (John Hunter's original term) or subsidiary mover. This suggests there must be similar degrees of antagonism. A muscle which by isometric contraction assists the movement by controlling the position of a joint other than the joint in question may be termed a fixation muscle (fixer). This terminology avoids the use of the word 'synergist' as, taken in its widest sense, all muscles other than the prime movers are synergists.

In any one movement there may be more than one agonist and more than one antagonist or, under what might be termed normal stress, a secondary mover may be capable of assuming prime activity, and experimental evidence (*e.g.* Stewart, 1937) has shown that following section the action of the alternative may be stronger than that of the normal prime mover. Nevertheless, study of movement does suggest that although a muscle may be designed for more than one purpose, and that this facility may provide for emergency measures inherent in the make-up of the species, it has really only one major action responsibility. A similar analysis might be made of selective muscle group activity, but here the problem is somewhat different, for the developed use of a particular set of muscles may be associated with the employment of a particular mode of progression, not as an alternative for general purposes.

It is well known that movement involving a joint may be represented mechanically in terms of levers, when the joint represents the fulcrum or centre of movement, the muscle the power, and the part to be moved the weight. Further, it is well known that there are three orders of levers. In the first order the fulcrum is between the power and the weight and, provided the power arm is greater than the weight arm, it works at a mechanical advantage; this type of lever is not uncommon in the body and is usually associated with an act of extension. In the second order the weight is between the fulcrum and the power; it is not a common body lever, is associated with strength and works at a mechanical advantage. In the third order the power is between the fulcrum and the weight, and it therefore works at a

mechanical disadvantage. It is a lever of velocity, is associated with flexion and is commonly found in the body.

Statements such as the above relate to principles of elementary mechanics: with the machine it would be profitable to take the story further, making allowance for moving bars, multiple levers, pulleys and all other factors influencing lines of force and resistance, in the sure knowledge that analysis would be rewarded by results of mathematical accuracy. With the animal, however, the problem is somewhat different. There is the difficulty in assessing, with any degree of accuracy, such factors as movement in space, summations of two- and three-joint movements, the modulating effect of sesamoids, of tuberosities and other projections acting as pulleys, and above all perhaps of physical changes in muscles. Study on this aspect of locomotion in man has attracted many workers, among them ELFTMAN (1938; 1939 a-d; 1940), while STEINDLER (1935) has written a book on the mechanics of locomotion in man; but the lower animal is a less tractable subject. Gray (1944) has given a lead by discussing the principles, and MANTER (1938) and BARCLAY (1946, 1953) among others have published experimental data; but with our present state of knowledge it is doubtful whether too deep a mechanical analysis will profit the average student of animal locomotion. Much the same remarks could be applied to observations on the centre of gravity of a limb or the whole body of a moving quadruped. The position varies with such rapidity, *e.g.* with changing footfalls, that only general statements can be made.

Of the part played by the nervous system in movement only the beginning is said when it is remarked that it controls the action of units in a locomotory act. As more locomotory units are brought into play so is the responsibility of the nervous system increased. It is not, however, within the scope of this chapter to discuss the detailed anatomy and physiology of the nerve tracts and impulses involved. The word 'control' is still valid whatever the locomotory circumstance and whatever the pattern of nervous response. In simplest form a motor unit represents axonal fibres of a motor nerve cell in the cord plus the muscle fibres it supplies, and in general it may be said that the number of nerve fibres in the unit is great in those associated with powerful limb muscles. Sherrington has shown that movement is possible only by reciprocal innervation of muscles. When a muscle contracts, an impulse (afferent) of relaxation passes to the opposing muscle. This explains why muscle bound does not occur, and exemplifies the fact that muscle relaxation is an active state. Indeed the moderating effect of the antagonist is as vital to the movement as contraction of the prime mover. Afferent nerve stimuli are concerned also with proprioception. Sensory nerve endings are present about muscle spindles which react to tension. Their

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particular arrangement in the muscle spindle is such that this stimulus operates only during relaxation, whereas similar terminations in tendons respond to tension transmitted from the muscle during contraction. These nerve endings are represented as essential aids to posture and are plentiful in the muscle units responsible for this purpose.

There are cases of incoordination in animals which are not characterized by disability to use muscle groups. During progression the parts are freely used but are out of phase, for example, the fore limb is extended before the shoulder region has completed swinging forwards. Naturally the entire gait is disturbed and the true symptoms are apt to be masked, but it would appear likely that these are instances of failure in the special afferent mechanisms of the nervous system.

This brief review of units of the locomotory system in terms of locomotor ability has indicated their potential, and it is now necessary to consider aspects of activity in the limbs and vertebral column, thus leading to considerations of whole body movement. In regard to the efficiency of the living machine Elftman (1939a) has said the following: 'Considered as a locomotor mechanism, the human body represents a compromise between the principles of physical efficiency and the dictates of sound anatomical structure': the same is true of the domestic animal.

THE LIMBS

When discussing movement of individual joints of the vertebrate limb it is reasonable to employ the terms flexion and extension but, as pointed out by Gray (1944), there is difficulty in defining overall movement in this way, since a summation of movement of individual segments adding up to overall flexion or extension would not necessarily relate to the state of the individual segments. He therefore suggested as terms for definition protraction for movement of the whole limb forwards (cranially) and retraction for a similar movement backwards (caudally) in the longitudinal vertical plane. There is less fear of ambiguity in defining overall movement in the transverse vertical plane as abduction or adduction, although it must be admitted the position of individual limb joints may be at variance from time to time. From the point of view of forward progression, the transverse movement is not of great consequence in domestic animals.

The complete action of all four limbs constitutes a locomotory cycle, and the complete action of any one limb a stride. For the purpose of analysis it is customary to divide the stride into phases coincident with definite stages of the locomotory pattern; thus during each stride a limb passes through two phases, a phase of elevation (protraction) when the limb is carried forwards on the body, and a phase of contact (retraction) when the body moves forward on the

limb while the foot remains on the ground. At the walk or trot the position of one limb, fore or hind, relative to its partner, is always constant, as when one is elevating, the other is at a comparable stage of contact. In accordance with the requirements of support there is a brief moment at the slow walk (*see also* section on gaits) when both members of a pair are in contact with the ground—exchange of contact. This moment is associated with a change in direction of body roll and, therefore, with the position of the centre of gravity.

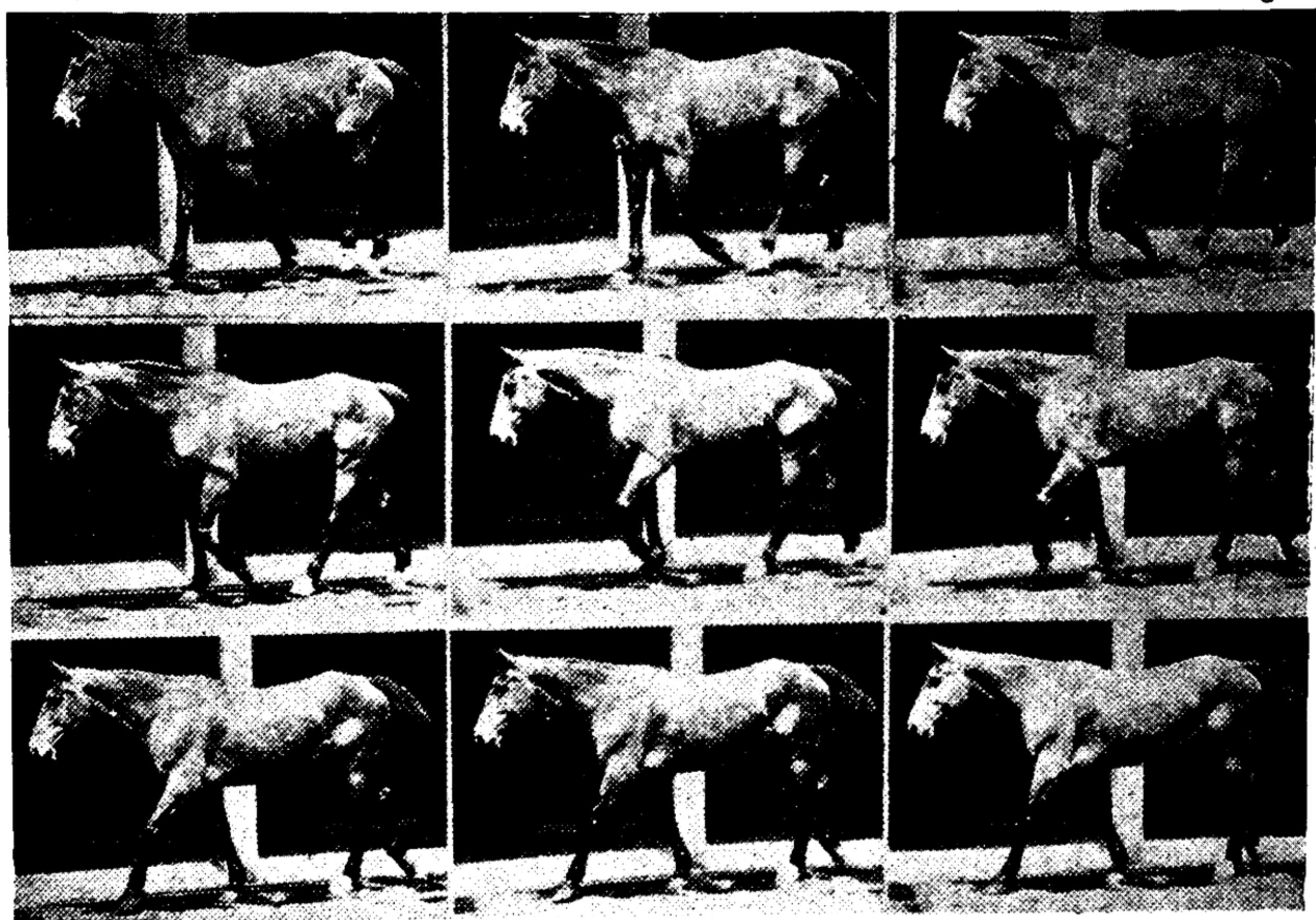


Figure 14.1. Selected ciné frames of the horse at the walk during all periods of the phase of elevation (protraction) of the left fore limb. The left hind limb has completed the period of cranial rotation and is demonstrating the period of extension during the phase of elevation: during the phase of contact (retraction) it is accommodating to first contact and preparing for propulsion during the maximum weight-bearing stage. Read left to right across the page.

If displacement of individual joints within overall limb movement is to be considered it is necessary to subdivide each phase (*Figures 14.1 and 14.2*). Owing to the individuality of the gait, and even to variations which may be witnessed in the same animal during almost consecutive strides or cycles, it is impossible to define periods which do not allow of overlap; but allowing for this and remembering that each period will last but a fraction of a second, it is possible to make arbitrary divisions of a continuous movement for convenience of description and for discussion of regional activity. During the phase of elevation from full retraction each limb passes through three periods:

a period of flexion of limb joints when the limb is picked off the ground; a period of cranial rotation* when the limb is carried forward on the body pivoting at scapulo-thorax junction or hip joint, with the majority of other joints fixed; and a period of limb extension at the conclusion of or immediately following which the limb is again placed on the ground.

During the phase of retraction each limb also passes through three periods: a period of first contact, when the prime duty of the limb is to accommodate to impact with the ground prior to bearing

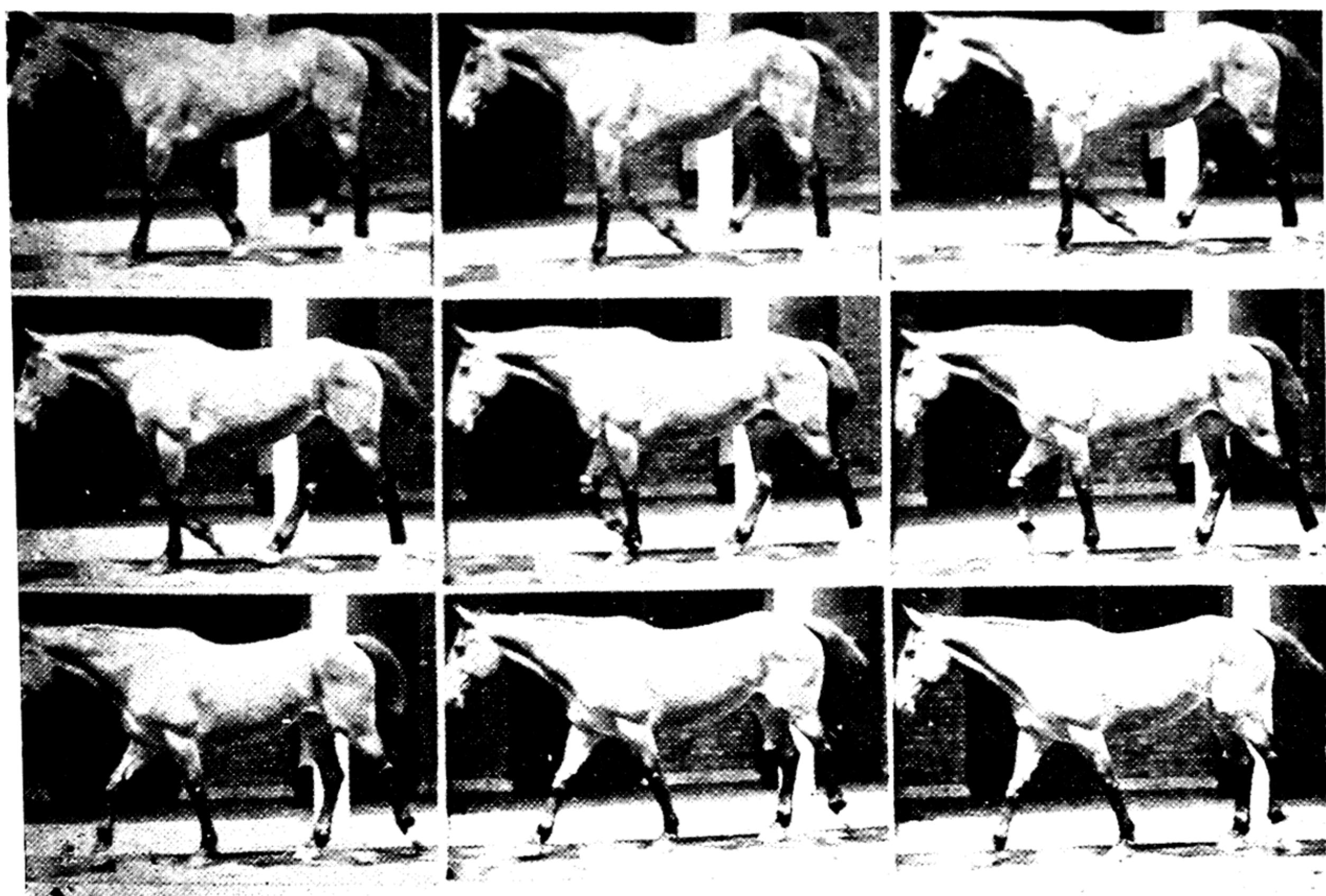


Figure 14.2. Selected ciné frames of the horse at the walk continuous in series with *Figure 1* during all periods of the phase of contact (retraction) of the left fore limb. The left hind limb has accommodated to maximum weight-bearing and is demonstrating the period of propulsion to full retraction and the period of flexion of the phase of elevation (protraction). Read left to right across the page.

full weight (GOUBAUX and BARRIER, 1892, refer to this as the period of 'attenuation of concussion'); a period of main weight-bearing when the limb passes over the vertical; and a final period, that of propulsion. This last should perhaps be referred to as the period of main propulsion as at all times during the phase of contact, when the limb has passed the vertical, it is assisting in propelling the body forwards. This sequence is clearly visible if individual frames of a ciné film of an animal at the

* It should be stressed that use of the word 'rotation' here is appropriate to movement of the scapula or femur in the sagittal plane of the body. It does not mean rotation on the axes of the bones.

walk are studied, and although not so obvious when viewed at faster paces, the sequence pattern is precisely the same. What does vary in the paces is the degree of angulation of joints of any one limb, the duration of periods, and the time intervals between periods and/or phases, which reflects on the position and placing of limbs relative to one another. No better example of this is seen than during the jump of the horse when, immediately prior to take-off, fore limb joints are quickly and strongly flexed, while the hind limbs are poised taking full weight prior to the thrust necessary to propel the body over the hurdle.

FORE LIMB

Review of Anatomical Features

The outstanding anatomical difference between fore and hind limbs from the point of view of movement is the nature of contact between limb and body. The fore limb is joined to the body by muscle only, but it is a union which allows freedom of movement. The comparative anatomy of the shoulder girdle musculature is steeped in evolutionary history; so far as it influences locomotion in cursorial mammals, it may be said that the resulting form, while accommodating to the needs of support, allows muscle groups about the shoulder to assist in moving the limb in protraction and retraction. Indeed, the manner in which scapula and humerus are bound to the chest wall in the absence of a clavicle, or at least an articular clavicle, would hardly allow of movement in any other direction. Thus, in these species, movement of the limb is concentrated in one direction, whereas in species in which an articular clavicle is present movement is possible in many directions. Further, non-clavicular forms allow of a single muscle, the brachiocephalic, derived from cleido-mastoid with part of trapezius plus cleidobrachialis, to pass direct from head to arm. This muscle is a powerful limb protractor. Another feature of the scapulo-thorax junction is that it permits of what may be described as 'scapular glide'—movement of the scapula either cranially and caudally or dorsally and ventrally. This glide may be due to muscle action only, but it is more often due to velocity and weight, *e.g.* the velocity and weight of the limb swinging forward in protraction or moving upwards as a result of impact with the ground. It is well known to any rider who places his hand on either side of the saddle that the scapula will move up and down as a horse proceeds over uneven ground. In this sense the scapulo-thorax junction acts as a shock absorber, not unlike a spring. There is little doubt that scapular gliding is an important factor in locomotion. It lengthens the stride, a feature associated with lateral movement of the vertebral column in many lower classes of vertebrates structurally unable to exhibit this type of scapular movement, and it generally assists in co-ordinating fore limb and trunk

movement. The degree of cranio-caudal gliding will vary with positioning of the limb and the species nature of the lateral thoracic wall. The elbow joint is a true hinge, and its working in this regard is aided by fusion of the radius and ulna. With reduction of the digital formula the arrangement of the musculature from the elbow distally need provide only for flexion and extension of all joints of the manus, although the conformation of these joints will allow of slight lateral movement (abduction and adduction) as required.

Summary of Phase Activity (see Figures 14.1 and 14.2)

Precise movements during any one stride, fore or hind, are not constant, but they are sufficiently regular to allow a summary of fore limb movement at the walk as follows. During the period of flexion of the phase of elevation the prime need is to clear the leg of the ground, and in this movement of the humerus—a means of flexing the shoulder—is of importance. During cranial rotation limb joints, including the shoulder joint, are fixed while the limb is carried forwards by the action of muscles of the shoulder-trunk region, that is to say, muscles extrinsic to the limb proper. This is the real act of limb protraction, with the scapula pivoting on its long axis, the humeral extremity moving cranially, the vertebral extremity caudally. Towards or at the end of this period of cranial rotation the digital and carpal joints commence to extend, followed during the next period by further extension of the carpus and then the elbow and shoulder in that order. Full protraction is perhaps more noticeable at fast paces when it is completed before the limb actually touches the ground. The method of extension of the shoulder is especially noteworthy: following cranial rotation of the limb with the shoulder joint fixed in a state of flexion the humerus continues to move cranially while the scapula retards, thus extension is begun but the final act is associated with the commencement of scapula rotation in the opposite direction, *i.e.* with the vertebral border swinging slightly cranially. This act is probably due primarily to the supraspinatus muscle, and it places the joint in the most advantageous position to receive weight. The phase of elevation is now over and it is at this stage when, at the slow walk, both fore legs remain momentarily on the ground.

During the period of first contact the limb is acting as a brake while accommodating to impact. The digital joints, particularly the metacarpo-phalangeal in the digitigrade animals, dorsiflex or over-extend. The general position of the joints varies little during the maximum weight-bearing stage as the limb passes over the vertical and the body passes over the limb, agonist and antagonist groups being seemingly jointly engaged as much as anything in preventing collapse of the limb; but the scapula has continued to rotate with the vertebral border moving cranially and the elbow to become more caudal in

relation to the shoulder. This prior positioning of the elbow, which in fact effects a flexion, is of value to its act of extension during the concluding period of retraction, that of propulsion. The propelling action of the fore limb is not great, particularly at the slower paces; indeed, as has been suggested above, its function during contact when there is less individual joint movement is more like that of a resilient prop, but the propelling power it has is associated with extension of the elbow. This is achieved by the powerful triceps muscle. It is reasonable to assume that other large muscle groups, suitably positioned, will stand out as being of importance during critical periods of movement, and analysis and experiment to determine group responsibility during all stages of body movement have engaged the attention of the functional anatomist. It is not the intention, however, in this chapter to give detailed consideration to studies of this kind, either now in regard to the fore limb or later for other regions of the body. Nevertheless, mention should be made of the prime action of manus extensors and flexors during the periods their names suggest, of the latissimus dorsi and teres major during flexion of the shoulder, and of the brachiocephalic during all but the first period of the phase of protraction; while the serratus ventralis, expanding as it does in many directions between scapula and trunk, serves as a valuable aid to shoulder rotation, control of scapular gliding, and support of the limb on the trunk.

HIND LIMB

Review of Anatomical Features

The pelvis is joined to the vertebral column by close ligamentous and/or osseous union so that, although pelvis, sacrum and tail may move on the remainder of the vertebral column, movement between sacrum and pelvis is negligible if present at all. This focuses attention on movement of the hip joint. The hip, as the shoulder, is deeply embedded in muscle and the femoral head, as the humerus, is confined within a cotyloid cavity; but although the pelvic bone moves less than the scapula—there is nothing comparable with a 'scapular glide'—the femur is capable of moving more freely than the humerus, particularly in abduction or adduction of the hip. The femoral trochanters have marked influence on the act of abduction as well as on flexion and extension, for attached to them are the gluteal muscles. In many species these muscles co-ordinate movement of the haunch with that of the lower limb, rivalling in this respect the powerful biceps femoris muscle. In the Equidae the expansive attachment of this latter muscle to the sacrum in addition to the ischial tuber presents it as a factor of some moment in movement at the lumbo-sacral junction, so characteristic of these species.

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The compound stifle joint is an area of great locomotory importance as may be seen from even cursory examination of its anatomy, and as reflected in the frequency of lameness originating at this site. The plane of movement in this joint is chiefly that of flexion and extension and the ligaments and menisci assist in maintaining apposition of its component parts as they do in controlling rotation on set axes. There are muscles attaching on the distal extremity of both aspects of the femur, and these gain attachment on similar aspects of the metatarsal or tarsal bones. Their arrangement and action is such that movement of stifle and hock is synchronized in flexion and extension, there being insufficient one-joint muscles in the hind limb of the larger domestic species to effect independent movement. The general arrangement of musculature of the pes is in accordance with that of the manus.

Summary of Phase Activity (see Figures 14.1 and 14.2)

At first sight, phase and period activity of the hind limb during movement, as exemplified by analysis at the walk or slow trot, may appear different from the fore limb, but if the limb is viewed from the moment the leg leaves the ground it will be found to be fundamentally the same. During the period of flexion the limb breaks without the facility of the pelvic bone being able to move on the vertebral column, although the whole pelvis will rotate towards the side being flexed when weight is released, an act not dissimilar in principle from the slight downward movement of the scapula with release of weight. The period of cranial rotation when femur flexes or protracts on hip (as compared with movement of scapula on chest wall), the remaining joints fixing, is quite evident, especially if at the time the poised hock joint is observed. Extension, as with the fore limb, commences in the digital region, and it is only nearing the conclusion of the period of extension that the hip is noticed to have commenced extension. The degree of extension of lower hind limb joints at this stage is not usually so great as at the comparable stage in the fore limb, unless the limb is to be placed far under the body, nor are they so fully extended as during the period of propulsion to follow.

During the period of first contact all joints are well ordered to allow for the characteristic 'spring' action so well adapted to take up the strain; indeed, every limb should be in a position to break speedily during any stage of contact with the ground, an inflexible member would be useless. As more weight is taken on the limb the hip continues to extend and the limb to 'push on' the body as propulsion is continued during the concluding period; for other limb joints, which had flexed to a degree while accommodating to the requirements of weight bearing, now also extend.

Comment on the more important muscle groups of the hind limb would suggest that during the period of flexion the hamstring group

of muscles is primarily engaged, while during cranial rotation the main activity passes to the psoas with gastrocnemius and tibialis anticus engaged in fixing, or initiating fixation, of the remaining joints. Neither hamstring muscles nor rectus femoris can be engaged in this fixation as the hip is moving. During first contact, and as the leg is



Figure 14.3. Selected ciné frames of the ox at the walk to show similarity of pattern with that of the horse. In these photographs the left fore limb is demonstrating the concluding stage of the period of flexion and the periods of cranial rotation and extension of the phase of elevation. The left hind limb has completed the period of extension of the phase of elevation and is demonstrating the period of first contact and the initial part of that of maximum weight-bearing during the phase of contact. Read left to right across the page.

approaching the vertical, the large gluteal muscle is effecting extension of the hip and the propulsive effort is reinforced with the femoral quadriceps and gastrocnemius muscles outstanding in extending stifle and hock respectively.

While the prime importance of some units of the system may be said to be their ability to effect the actual movement, it is equally true that others are as valuably engaged primarily in steadyng the movement or maintaining posture. There is, of course, no absolute division of labour and the same units at different times serve all these purposes. There is, nevertheless, a degree of selective use. As many of the domestic species spend a considerable part of their life standing, examples of these postural agents are much in evidence, particularly in the limbs (*Figure 14.4*).

A feature not peculiar to these species is the overlap of insertion of

one muscle or muscle group with the origin of another, but this is of particular significance in a weight-bearing limb. The solidity of the elbow is strengthened by the fact that prime elbow flexors, biceps and brachialis, insert on the radius while manus extensors originate from the distal extremity of the humerus. In addition there is a strengthening band of fascia, the so-called *lacertus fibrosus*, connecting biceps with the origin of the common digital extensor across the dorsal aspect of this joint, of value to both movement and support. The fore limb of the quadruped, as exemplified by the horse or ox, will 'break position' or flex on the volar side towards the belly. To assist in resisting this tendency at rest, that is to say to maintain posture, it is noted that on the dorsal aspect an extensor muscle is inserted immediately distal to the joints concerned, carpal, fetlock, metacarpo-phalangeal and pedal. There are also in the limbs of these animals strong fascial bands passing from bone to tendon, the so-called 'check ligaments'. The tendons of the major flexors of the foot receive such reinforcing bands above and below the carpal and tarsal joints. As the tendons to which they are attached pass to an insertion distal to the fetlock joint, they serve to check dorsiflexion or over-extension of this joint and thus relieve strain on the tendons of insertion.

Another important structure in maintaining the state of the fetlock is the modified interosseous medius of the third digit. In a pentadactyl limb, such as that of the dog, the metacarpo/tarso-phalangeal joint is not far distant from the ground, thrust on the foot is shared by all digits, and lateral movement between the phalanges of all digits is possible. The interosseous medius muscles of the digits are fully fleshy and play an important part in these movements. With the horse and ox the foot is more digitigrade; there are less digits to receive weight, and interdigital movement, at least in the horse, is restricted. Accordingly the single interosseous medius muscle of the horse, commonly known as the suspensory ligament, is almost entirely replaced by tendon fibre, and that of the ox is so to a large extent. That some fleshy fibres should still be present in the interosseous medius of the ox is understandable both on evolutionary and functional grounds, the metacarpal/tarsal bone represents fused elements and two fully developed digits are present on each foot. The interosseous gains a major attachment on to the sesamoids on the volar aspect of the joint, but slips are continued round the joint attaching to one of the extensor tendons. The precise function of these extensions is not clear, but they cannot do other than assist in bracing the joint. The modified interosseous muscles of these species are ideal for maintaining the erect state of the fetlock joint. Histological examination does not reveal elastic fibres in any number, but they are capable of stretch. This property is demonstrated whenever the limb comes to the ground and the joint is dorsiflexed or over-extended, as is witnessed by the

presence of mud on the tuft of the fetlock of a horse walking on grassy, but not necessarily very soft, ground. Further, when rebounding from the stretched condition, they give a powerful release-action aid to picking the leg off the ground.

Of bone/ligament relationship aids to posture there is no better example than the so-called 'patellar lock' of the horse. The medial lip of the femoral trochlea is very prominent and is surmounted by an articular boss. When the quadriceps musculature contracts in

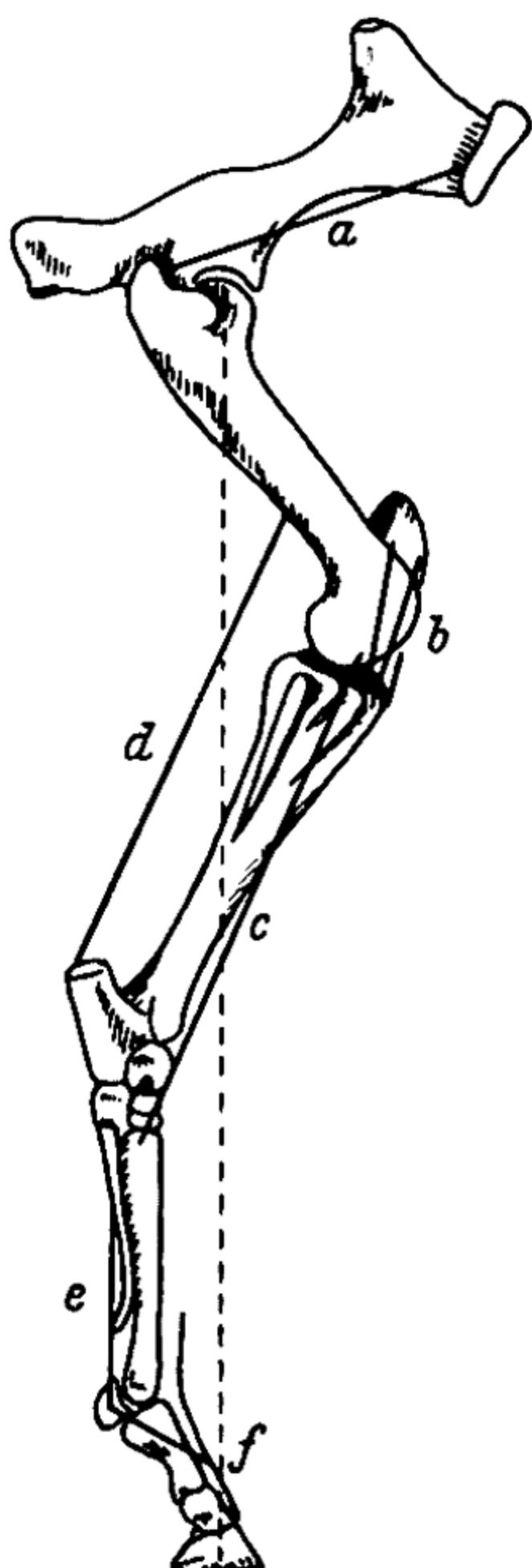


Figure 14.4. Skeletal drawing of the right hind limb of the horse showing the position of less fatiguable structures which assist in maintenance of posture (modified from Zietzschmann, 1910).

- a = tendinous core of the middle gluteus muscle
- b = the straight patellar ligaments
- c = peroneus (fibularis) tertius
- d = superficial digital flexor (plantaris)—as far as tarsus
- e = interosseous medius muscle (suspensory ligament) with slip joining
- f = terminal portion of the tendon of the long digital extensor

extending the stifle of a horse the patella glides upwards and tips at first laterally and then medially, as is directed by the prominent medial lip, and comes to rest on the articular boss and surround. The arrangement of femoro-patellar and straight patellar 'ligaments' is such that the joint is then locked. The more powerful the flexing force in the longitudinal axis of the limb the tighter becomes the lock. This mechanism has been described by SHUTTLEWORTH (1944). There is no doubt as to its working with a horse at rest, as may be noted when weight is shifted from one leg to another, but whether a partial or complete lock is momentarily engaged during each stride would appear to be a matter for further enquiry. The only manner in which the joint may be unlocked is for the patella to move in a reverse direction from that described for locking. It must first be pulled laterally and it may then glide downwards and medially. It

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would appear that the biceps femoris muscle, in virtue of its attachment to the patella, working with the tensor fasciae latae, is responsible for this lateral pull. So interesting a mechanism prompted enquiry of a parallel working in other species. The femoral trochlear lips of the bovine are certainly unequal in size but the shapes are not entirely suitable, and the ox does not appear to lock the patella in this way while resting. The only other skeleton observed by the writer with a similar irregularity of the trochlear lips is the giraffe; it has not been possible to palpate this region in a living animal, but examination of a cadaver does suggest there is some form of patellar lock. It should be mentioned that these remarks apply to animals which of anatomical necessity hold the stifle joint in a state of semi-flexion during rest, and therefore, while standing have a greater responsibility in balancing the state of this joint—one of the most important for movement in the whole body—against the flexing force of gravity. Reference has already been made to synchronization of stifle and hock joints in movement, and the same is true at rest. So far as the horse is concerned this is effected by the largely tendinous content of the peroneus (fibularis) tertius and the superficial digital flexor (plantaris), which pass from distal femur to tarsal and/or the large metatarsal bone, although the plantaris continues from an attachment on the tuber calcis to an insertion more distal on the limb. They function as two inelastic strings constituting with the bones and joints concerned a parallelogram of forces. That these two muscles function in a similar way in other animals, for example the ox, and yet do not contain the same content of tendon fibre, is associated with the fact that the horse remains standing for longer periods than the ox and, therefore, the minimum of fatiguable structures is present in the limb. Once the stifle of the horse is fixed, the hock is fixed, and the state of the fetlock is maintained by tendinous structures, *e.g.* the modified interosseous medius muscle (*see Figure 14.4*).

THE VERTEBRAL COLUMN

The part played by the vertebral column in movement has not received close attention, at least in so far as being complementary to discussion of the part played by the limbs. The vertebral column as a biological structure has been the subject of an exhaustive review by SLIJPER (1946). Slijper considers the form of bone, ligament and muscle in many species of mammal, and much is relevant to the domestic species.

Reference has been made to the processes of the vertebral column in the sense that their arrangement accommodates to the requirements of support and movement, and in general it may be said that this is an

arrangement which restricts lateral bending and allows of forward progression. The classical difference between the column of the quadruped and the biped is, of course, the development of the dorsal spines (spinal processes) of the thoracic vertebrae where, in the quadruped, their length is associated with support of the head. Again, the nature of the articular processes is significant. According to Slijper, of particular moment in animals which bend the mid-back region is the change in direction of the slope of these facets at, or near, the point of maximum bend. This is associated with the phenomenon of what has been styled 'anticlinaly', the change in direction of neural spines, which is also discussed by Slijper.

The close musculature of the back consists of a series of small muscles passing between the processes of adjoining vertebrae. They retain the segmental arrangement typical of the somite, and their action is restricted to that about a single joint. There is more than one series of muscles, and two vertebrae may be connected by as many as six small muscles passing in various directions. From a mechanical point of view it might be thought that such an assembly represents a good example for accurate analysis of the forces involved in a movement. An isolated joint, with less important muscles removed, well illustrates the opposing action of muscles working on the same lever arm. Nevertheless, the very complexity of the complete unit and the fact that from the point of view of total movement no one intervertebral union can be considered in isolation, suggests that all that need be said here is that these muscles effect a bending action on the column while allowing for necessary tensions; in this sense the column may be regarded as a flexible rod. Superficial to the close musculature are the powerful muscles of the column such as the longissimus dorsi which, although retaining evidence of segmental origin as demonstrated by attachments to numerous vertebral processes, passes also as a mass from one area to another. Many of these muscles have attachments to regions other than the vertebral column; the longissimus dorsi itself attaches to the ilium of the pelvis, but perhaps the most important extrinsic muscle, from the locomotory aspect, is the psoas major. The psoas passes from the ventral aspect of thoracic and lumbar vertebrae to the femur, it is thus able to flex the hip in addition to acting on the spine. Yet other extrinsic muscles of the column pass to more distal areas of the limb, providing means for co-ordinated effort between limbs and body.

The cervical region presents a series of muscles passing from head and neck to sternum and fore limb which aid in flexing the neck, and a series on the dorsal aspect passing to the dorsal spines of the more cranial thoracic vertebrae. These dorsal muscles are more distant from the vertebrae and in their course they flank the powerful ligamentum nuchae. They, with the ligaments, serve as a means for

support of the head. A property of the ligamentum nuchae is an abundance of elastic fibres; thus it allows of more stretch than the normal ligament and in recoil is an active means of assisting muscles in lifting the head. It so happens that the slope of the dorsal spines to which these cervical muscles are attached is such that their fibres of attachment are at right angles, or nearly so, to the long axis of the spine. Slijper (1946) has examined this arrangement in a number of species, and offers his findings as evidence to support his suggestion that the most favourable direction of dorsal spines is the direction perpendicular to that of the muscle and ligamentous forces acting on them; this being an observation on the vertebral musculature as a whole, not just the cervical region. Slijper continues by accepting the fact that few, if any, dorsal spines receive the attachment of but one muscle. He therefore concludes, in general terms, that if more than one muscle is attached to a spine, the slope of the spine will be intermediate between the line of two muscles if they are of equal importance, and perpendicular to that of highest importance in other cases. The estimation of importance is based on the thickness of the muscle and the position and extent of its area of attachment. When, however, the large number of muscles attached to the dorsal spines is taken into account, there must be instances of powerful muscles accepting a compromise position in Slijper's sense of the word. It must also be remembered that the line of attachment will vary with the movement. What is perhaps more to the point is that the dorsal, or neural, spines act as a series of closely co-ordinated levers, and what is really of consequence is the summation of all forces acting upon them, the conditions affecting which will be related to the slope of the spines. This does not necessarily destroy the concept of a most advantageous line of muscle attachment for effecting a movement.

Before further considering the vertebral column in posture and movement it is as well to consider the problem of suspension and equilibrium of the column in relation to the body as a whole. Of comparisons between the designs of Man and Nature few have attracted more attention than comparisons between the means of support of the mammalian quadruped and the construction of bridges. D'Arcy THOMPSON (1942), in his stimulating account, possibly following the lead of FIDLER (1909) on bridge construction, compares the design of a horse (quadruped) to a bridge of two balanced cantilevers. This is only a general statement for further analysis and Thompson elaborates on his suggestion, mindful of the fact that the two piers of the living bridge—the limbs—do not bear separate and independent loads, and that the two cantilever systems are unequal in magnitude and importance. The size and slope of the dorsal (neural) spines in all regions is of significance, and Thompson illustrates the nature of the spines in many animals in support of his theory. In regard to the

greater weight about the fore-end of the body, *i.e.* a forward centre of gravity, he instances this as of value to the greater propulsive effort of the hind quarters.

GREGORY (1937) in a more generalized review considers, as did Thompson, the legs as the towers, the backbone as the arched cantilever system that is supported by the towers, and the thorax and abdomen as the 'live load' (not referred to by Thompson) suspended from the arch. He gets over the problem of overweighting at the cranial end by suggesting the head and neck not as part of the cranial cantilever system, but rather that the bridge is continued in front by a draw-bridge, or jointed crane—the neck, which in turn supports a strange shovel-like contraption which moves—the head. The acquisition of a long neck and mobile head is an improvement on the primitive animal. Associated with the support of one tower is the modified pectoral girdle, and of the other the pelvis. A further comment is that only when shoulder and elbow became applied to lateral thorax, and pelvis further united to the vertebrae, was four-footed running possible without excessive lateral movement of the body.

Gray (1944) suggests that the inequality of the two extremities in so many species places the analogy of the two balanced cantilevers as a very specialized, and perhaps quite theoretical, case of a more generalized proposition, and offers the mechanical picture presented by a tetrapod as essentially that of a flexible overhung beam supported by four elastic legs. Further, he mentions the bracing effect of limb musculature supporting the column. The view of Slijper (1946), an extension of the theory advanced by BARTHEZ (1798), and later developed by STRASSER (1913), is not really opposed to that of Gray, although it varies in some respects. He compares the arrangement with a tied arch construction, the vertebral column and pelvis acting as the bow, the ventral abdominal musculature and sternum the string. He continues by discussing the interplay of forces acting on the bow and string as influenced by body weight, and concludes by stating that in this type of construction no force would be exercised on the two supporting piers in the cranio-caudal direction. Here Slijper differs from Gray in that he pays less regard to the part played by the retractors and protractors of the limbs in moving the bow.

Thompson mentions the tied arch construction, but as in this place he is referring only to the skeleton, which obviously does not possess the string, he does not develop it, which is a pity as his views on this would have been interesting. Slijper criticizes Thompson's double cantilever bridge, but this is not entirely justifiable as Thompson's words were not meant to be final on this particular issue. The weak point in Slijper's story is the anchoring of the string; caudally it is firmly attached to the pelvis, but cranially only to the first ribs. While admitting this, Slijper points out that the disadvantage

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is partly compensated for by the short length and comparative immobility of the first rib, and the possible fixation action of the scalenus muscle.

It is obvious that comparisons such as this must allow for body weight, and for the fact that the living bridge is intended to move. The emphasis placed by Gray and Slijper on a flexible rod—the vertebral column— influenced also by extrinsic factors, is therefore attractive. It is quite definite that, however suspended, the column must be regarded as part of the whole functional body unit, strong in itself yet capable of bending, and working in close harmony with the limbs.

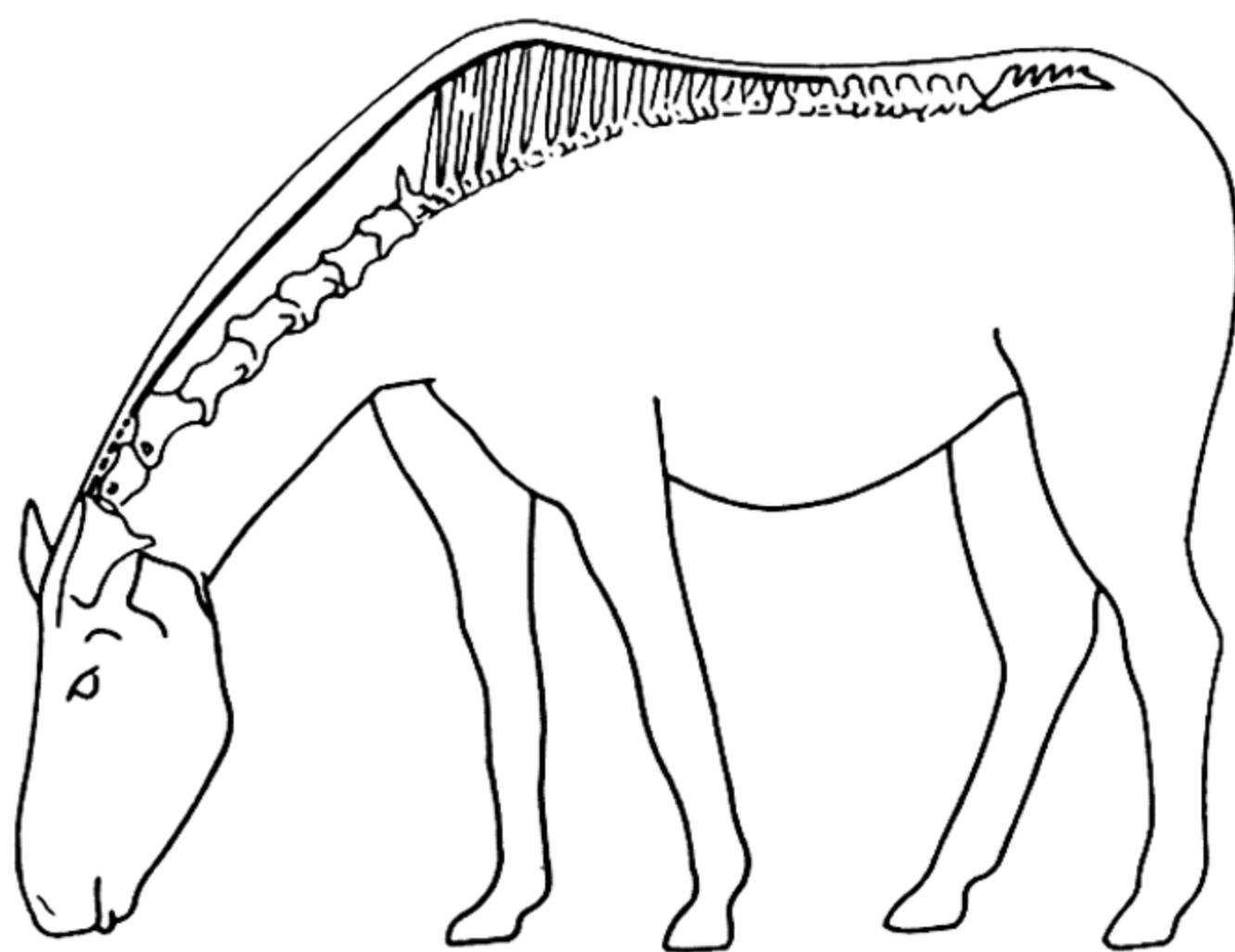


Figure 14.5. Schematic drawing of a grazing horse; note the straight cervical vertebrae in this posture and forward displacement of the fore leg. (From Slijper (1946) by courtesy *Verh. Akad. Wet. Amst.*)

In regard to activity of regions of the column, movement of the neck is dominated by movement at the atlanto-occipital and cervico-thoracic junctions. Strains on the cervical segments are relieved by muscle and ligament, and the ease of carriage of the head is associated with the degree of slope of the neck. The method of suspension of the head has been compared to that of a loaded beam supported at one end only. Movement of head and neck is associated also with feeding habits, and it may be noted that with increase of length of limb the horse is only just able to graze off the ground and at that it is customary to stand with one fore leg slightly advanced (*Figure 14.5*); the same is reflected in the posture of a young foal learning to graze with legs astride. When considering movement of the thoracic region, allowance must be made for the fact that the vertebrae are connected with the ribs forming part of the thoracic cage. And it would appear that collective movement of a group of thoracic vertebrae, as opposed to movement between any two individuals, is more possible, at least for the purpose of normal progression, in the more caudal members

of the region, *i.e.* those beyond the actual confines of the thorax proper, although there may be critics of this. Whatever interlumbar movement is possible will be mainly in the dorsal-ventral direction. So far as skeletal factors are concerned the degree and plane are influenced by, in the horse, proximity of the large transverse processes and the inter-transverse facets, and in the ruminant, cupping of the articular processes. The lumbo-sacral junction is articular but the sacral vertebrae are always fused forming a rigid structure roofing the pelvis.

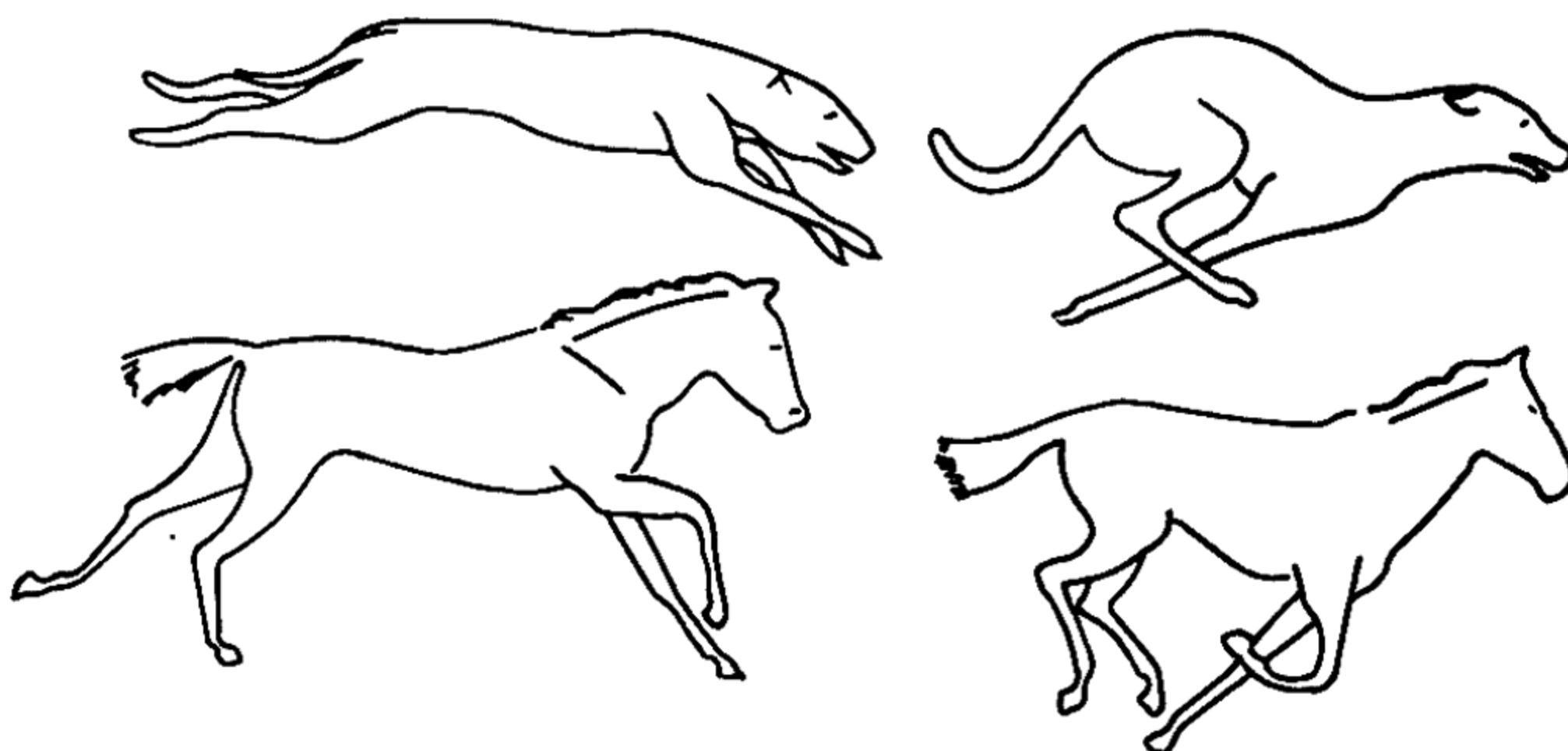


Figure 14.6. Trace drawings of two type animals, dog and horse, to show vertebral movement at the gallop. On the left phase of maximum stretch, on the right phase of maximum bend. (Modified from Slijper, 1946, from photographs by Muybridge, 1899.)

- The tail may also be regarded as a loaded beam supported at one end only, although its small size in the average mammal does not allow it to be compared with the head and neck in this sense; it is an accessory factor of balance.

It would appear, therefore, that any degree of movement of the back is possible in two areas only: the region of the thoraco-lumbar junction, and at the lumbo-sacral junction. Vertebral movements are more noticeable at speed, and it is possible to designate animals as adopting the 'leaping gallop' or the 'horse gallop'. The leaping gallop is typical of the carnivores and exhibits bending and stretching of the mid-back in the general region of the so-called 'diaphragmatic' vertebra (*Figure 14.6*). (For discussion on the significance of this vertebra, *see Slijper*.) One of the most important muscles associated with bending of the mid-back is that portion of the sacrospinalis muscle passing from the blade of the ilium to the last rib, the iliocostalis or the initial part of the longissimus costarum of many authors*; this muscle is well-developed in the dog. In animals exhibiting the horse gallop there is little bending of the back proper, a feature of value for draught purposes. The movement which does occur, and it is of great moment

* At the level of the ilium the longissimus dorsi and iliocostalis arise as a common mass, and this mass is referred to as the sacrospinalis muscle.

as it allows the hind limbs to be brought forward under the belly, is at the lumbo-sacral junction (*Figure 14.6*). The horse itself, as might be expected, shows this well, and there is muscle accommodation. Of particular value is the attachment of the biceps femoris to the sacrum as well as to the tuber ischii, for the sacral attachment allows this muscle to 'open' the lumbo-sacral joint. A muscle conspicuous by its poor development in the horse is the iliocostalis. The arrangement in the ox is of interest; an iliocostalis muscle is present, though not so well developed as in the carnivore, but the biceps femoris has no independent attachment on the sacrum, its most proximal fibres being attached to the tuber ischii. The ox does not markedly bend any region of the back, either mid-back or at the lumbo-sacral junction, and when observed at paces other than the walk will be seen generally to move the back as a whole, pivoting on hip or shoulder. These observations do not tally entirely with the account given by Slijper, who does not feature the iliocostalis as of value in the leaping gallop, and refers more to the action of the longissimus dorsi than to that of the biceps femoris as being the major factor in influencing lumbo-sacral movement; in other words, that the joint opens more from a cranial than a caudal pull and that the bringing of hind limbs under the body is not associated with this particular action. But in fact many animals which have an attachment of longissimus dorsi to the sacrum, among them the ox, do not exhibit marked opening of the lumbo-sacral joint.

ADAPTATION FOR SPEED AND POWER

Many authors have written on the theme of adaptation for speed and power in the vertebrate body, but few have covered so wide a field as BRAZIER HOWELL in his book *Speed in Animals* published in 1944. Howell has traced in masterly fashion those modifications of form which, associated with or determined by changing function, have resulted in the shape of speedy animals; of these the ungulates, because of our knowledge of them, figure as frequent examples. His observations are not confined to the mammals, he refers to specialization in units of the locomotory system in all the main vertebrate groups; but these specializations may be regarded, if one so desires—and it is so indicated, as a build up to an appreciation of the refinements in the speedy mammal, and it is particularly for this reason that Howell's book should be consulted.

SRINIVASAN (1944) has written of the horse 'The specialization for speed necessitated changes in the form and general appearance. The horse has its body moulded externally in such a way as to offer least resistance to the air, the medium through which it has to pass. The body, head, and neck are smoothly rounded with no needless excrescences and with perfect symmetry of form. The same kind of symmetry is maintained in the limbs which are long and slender

distally with the massive muscles at the shoulder and hip where they blend with the contour of the body, their force being transmitted by long and slender tendons. This concentration of weight high on the limbs quickens the speed without diminishing the stride.' This is neither a profound nor an original statement; but it admirably sums up the position which has been stated by many and will serve as a basis for a brief analysis. The property of the vertebral column to combine rigidity with the ability to flex in the sagittal plane, well shown in species with legs set under and at right angles to the body, has already been referred to, and no length or slope of spine or process necessary to accommodate to the type of movement exhibited is such as will disturb the smooth contour of the back, a disturbance witnessed in more cumbersome forms. It is perhaps appropriate to mention here another function of the vertebral column, that of buffering in 'concertina-like' fashion against opposing thrusts initiating in the limbs. When the fore limb is first placed on the ground it acts as a brake, the scapulo-thorax junction will act as a buffer but the follow-through will be taken up by the trunk. Similarly a thrust coming from the hind quarters will be buffered by the column as the effect is transmitted along the trunk.

The contour of the neck, braced by the extensive ligamentum nuchae, is similarly well-set behind the streamlined head. The more expansive head with possible excrescences, and wide neck and brisket of the bovine, cannot be viewed in this advantageous light, but such are accepted locomotory handicaps in this species. The blending of fore limb with the body is associated with the lateral positioning of the limb and the absence of a clavicle—although it is true that absence of a clavicle is not confined to cursorial species. It may be re-stated also that this allows of a muscle assembly about the shoulder and arm suitable for efficient protraction and retraction. A most interesting assembly: symmetry, with short muscles for strength, longer muscles for movement and speed, although at this level of the limb not of the long tendon variety and therefore, as may be styled in this sense, dual-purpose muscles. Clear of the body, the fore arm first demonstrates the slendering effect more evident in the manus. Reduction of the ulnar bone is a characteristic of fast-moving quadrupeds, unless the ability to prone and supine is still required. In the larger domestic animals this is not so, and the reduced ulna is fused or closely connected to the larger radius, a feature of strength. The olecranon process, however, remains well-developed, as attached to it are the heads of the powerful triceps, the extensor muscle of the elbow. With reduction of the ulna the radius occupies more of the articular surface of the elbow joint, and this would appear to be associated with the directed plane of movement of the joint to flexion and extension, a feature in keeping with the well-developed olecranon lever arm and aided by

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fusion of radius and ulna, although Howell regards this latter point as a later refinement. This plane of movement, flexion and extension, is characteristic of all limb joints with the exception of, to a degree, the shoulder and more so the hip. Lengthening of the limb is achieved by modification of the manus: the foot, hoof enclosed, the fetlock raised, the metacarpus lengthened. With lengthening of the metacarpus comes lengthening of its associated tendons, but there is also reduction in the number of bones and of the tendons associated with them, a reduction not divorced from changes higher in the limb. This compacting of bone elements represents a modification for strength as well as speed, and it is interesting to speculate that rearrangement of muscle insertion is such that modified tendons still attach to the original bone of attachment, if still present, even though it be reduced in size and fused with another. Fusion of this kind, and the metacarpus provides examples, is functional and not pathological.

The arrangement of muscles of the hip is not dissimilar in principle from that of the shoulder. Here again is an area where short members, in this case the femoral hip musculature, consolidate strength, while larger muscles spread to effect their action in collaboration with movers of the lower joints, with all subscribing to maintain a suitable body contour not encumbered by a large tail. The sacro-pelvic union is in an entirely different category from that of the scapulo-thoracic junction. The latter acts perfectly as a shock-absorber, the former exhibits a solidity which, with the mobile hip and synchronized action of stifle and hock, allows the powerful thrust of a straightening hind limb to be transmitted *via* the pelvis to the trunk. Reduction of the fibula may be regarded in similar light to that of the ulna in so far as it is associated with modification of the pes and the plane of action of the stifle and hock joints. Modification of the pes is precisely the same in principle as that of the manus. It is true that tarsal bones are more closely knit together than carpal bones and that the other bones of the pes are more slender and larger than their manus counterparts, but this would all seem to be associated with the greater propelling power of the hind limb.

ANTICONCUSSION

Adaptation of the manus and pes throws emphasis on the need for an efficient anticoncussion mechanism in animals with a reduced number of weight-bearing digits. The aids to reducing concussion are first and foremost in the foot itself; but there are of course other factors such as the positioning of bones, the nature of joints and ligaments, the arrangement of muscles, the presence of special structures such as modified muscles in the lower manus and pes, and the general buffering effect of the tissues of the body. Of the bones an important part is played by those of the carpus and tarsus. Other than their duty

of increasing area mobility their general arrangement is such that, in this present respect, they are enabled to distribute weight in more than one direction.

The foot is an area of great biological interest and economic importance; in the latter sense particularly but also in the former it has engaged the attention of the veterinary surgeon and his predecessors since time immemorial. Again taking the horse as an example, the foot contains the pedal joint, with which is incorporated the distal sesamoid (navicular bone), and to the terminal phalanx are inserted the tendons of the main flexor and extensor muscles. The lateral cartilages, structures of significance to the mechanism of anti-concussion, are attached to the wings of the terminal phalanx. The highly modified integument forming the hoof is represented by the horny epidermis of the wall, sole, and frog pad, their associated coria, and the subcutis. The subcutis is irregular in distribution; in places it forms 'cushions', among which is the large digital cushion overlying the frog pad.

All of these integumentary structures are to a degree yielding, more so the digital cushion and frog. Smith (1912) talks about an elastic wall and an indiarubber-like pad and this is a fair analogy for their relative merits in this connection. The slope of the phalanges would require at the very least a caudo-ventrally placed pad in support, as indeed is present in less digitigrade forms such as the carnivore, the horse in fact has a pad and a highly developed cushion enveloped within the structures of the hoof. A flexible pad, we are told, was present in *Eohippus* and the toe had an independent covering, and SIMPSON (1951) has reviewed the history of the modifications of these integumentary structures, together with reductions in the digital formula, from that time to modern *Equus*. According to this author, from the Miocene when the foot became more digitigrade the pedal bone was covered by a more substantial appendage, the hoof, of which the pad became a part. During this period, when the number of digits was also reduced, accommodation to the now greater need for support of the more raised fetlock was provided for by the presence of ligaments attached to, and running proximally and distally from, the fetlock sesamoids. The former support represented, of course, the modified interosseous medius muscle of the third digit, the latter an organization of ligamentous tissue. Such is substantially the state of affairs in the modern horse.

According to this same author, if all structures of the foot, not just the bones, are considered, there were more profound changes in the Miocene than in any other period of the long story of the evolution of the horse. Simpson discusses also the possible use of the second and fourth metacarpals and metatarsals and their short digits in the sense that, if they were functionless, why did they persist for as long as

palaeontology recalls? His hypothesis is that at the moment of extreme over-extension of the fetlock during weight-bearing the short side toes would touch the ground and would, therefore, act as a buffer: with increase of strength in the supporting ligaments of this joint this need became superfluous and the bones then became reduced. A modern analogy with this type of mechanism in the functional as opposed to the evolutionary sense is recorded by a Swiss worker, LANDOLT (1945), when discussing the function of the accessory digits of the feet of cattle. In some Swiss breeds, Landolt mentions that the nature of the terrain presents the accessory digits (numbers 2 and 5) as a means of improving footholds, more valuable in hind than fore, and of preventing the feet from sinking too deeply into soft soil.

Sufficient has been said above to suggest it reasonable to consider two overall areas in the foot, the frog and the wall, as being involved in countering the initial effects of concussion, even though they be engaged almost simultaneously. The frog and digital cushion receive full weight as the foot is placed on the ground, compression is relieved by lateral expansion and the impact is taken up by the lateral cartilages and the wall of the hoof from the side. Then, as the foot pivots, more weight is received on the wall from the vertical direction. It should perhaps be mentioned that it is often only at the last moment that the heel is so placed as to be the first to contact the ground. Particularly at slow paces and again particularly with the fore limb, the foot is carried with a pointing toe. The sudden switch, if it occurs, can be regarded as a direct aid to anticoncussion and to the propulsive effort to follow. It should also be remembered that the horny structures are connected to the pedal bone by sensitive laminae and that the digital cushion is far more pliable than the pad.

Changes in shape of the horse's foot during movement have been studied experimentally since the latter half of the nineteenth century, and LUNGWITZ (1891) using electrical apparatus recorded that under weight the hoof dilates at the heels, at both the coronary and solar edges, and the sole sinks nearer to the ground; with this there is a contraction of the coronary band at the toe, and the bulbs of the heel—*i.e.* the digital cushion plus the adjoining part of the frog at its junction with the 'bars' of the wall—swell and incline backwards and downwards. As is to be expected, he found greatest response during times when the digital joints were over-extended, and these periods have since been proved and must then have been thought to be those associated with maximum weight-bearing. There is still no overall criticism of this general statement of change in form of the horse's foot during movement. Smith (1912) adds to this information by stating there is also a vertical compression of the wall which produces a diminution in its height.

Later workers have studied the structural arrangement in terms of

how it allows for and accommodates to these changes. The substance of the digital cushion abounds in fatty, white fibrous, and elastic tissues, hence little further explanation of its action is required: it is exactly the same mechanism as with the pad of the carnivore and rebound occurs when the foot is pivoted on to the toe. The lateral cartilages are situated partly within and partly without the cover of the hoof, they are composed of hyaline interspersed with fibrous tissue, and 'give' to and fro in the lateral direction as weight is received and released from the digital cushion. Their relation to the vascular structures is such that they assist, in valve-like action, circulation in the foot. In older horses of the heavier breeds it is not uncommon for these cartilages to ossify, the condition being referred to as 'side bone'. That this condition is indicative of unsoundness in a lighter and fast moving animal is an illustration of the value of the cartilages to anticoncussion.

Prominent among workers who have studied the epithelium of the hoof is BRUHNKE (1929), and it is not without interest that he was responsible for supervising the work in many of the forges in North-west Germany. In an account illustrating the functional significance of the architecture of body connective tissues in general he, along with Kruger, pays particular attention to the connective tissues of the foot (BRUHNKE and KRUGER, 1928). They refer to the parallel fibres of the sensitive laminae on the wall of the pedal bone, which interdigitate with the horny laminae of the hoof, as being in a direction to accommodate best to the vertical thrust on the limb. The horny laminae are, of course, part of the epidermis of this region and the underlying sensitive laminae are attached to a modified periosteum of the pedal bone. Other than the major laminae there are many secondary laminae, which give a feather-like appearance, placed at varying angles. This arrangement is more intricate in the horse than in the ox, as in the latter animal by far the greater proportion of primary laminae have no secondary foliation. Further, it is interesting to reflect that in areas where a part of the integument of the foot is in contact with bone there is no subcutis; whatever part of the corium is involved it is in direct contact with the periosteal layer. The laminar line is not necessarily straight and, in addition, the hoof has angles of contact with the sole, heel and frog. In a parallel article BRUHNKE (1928) discusses the varying slope of the secondary laminae and the thickness of the primary laminae which accommodate to these slopes, to the play of the extensor and flexor tendons and to movement of the pedal bone. In this same article he refers to the ox; the lateral wall of the hoof of the ox is thicker and more round than the interdigital wall, also a more intimate contact exists between the hoof and the corium at the coronary region. Appreciable weight is taken on the medial wall at the interdigital cleft, and here both on the wall and sole it is interesting to note

that elastic fibres predominate. These observations serve as a corollary to those on the horse.

Other than the laminar corium attached to the periosteum of the pedal bone, the perioplic corium exists to nourish the periople—the varnish of the wall—and the coronary corium to nourish the bulk of the wall. The horny laminae of the wall are in contact with the laminae of the laminar corium and the two are connected by uncornified cells of the secondary epidermal laminae, the product of the deeper layers of the coronary corium. In this regard, in HABEL and BIBERSTEIN's translation (1952) of TRAUTMANN and FIEBIGER (1949) there is added a quotation from the work of BAIER (1950), who stresses it as important to distinguish between the term 'sensitive lamina' and 'dermal lamina'; the uncornified layer of the wall is adherent to the laminar corium and the two make up the sensitive lamina.

Turning now to the wall proper, the epidermis, it is possible to distinguish three layers; a thin outer zone covered by a thin layer of periople, a thick middle zone and an inner zone in contact with the laminae. BRUHNKE (1931) has considered the nature of these zones in several domestic animals, and points out that, although the superficial layer is similar in the horse and ox, the deeper layers are not; further, in the ox it is difficult to separate corium from any part of the wall. He also mentions comparative growth of the tubular and inter-tubular horn, but not in any great detail, although he does refer to the greater degree of elasticity in the hoof of the ox as compared with the horse. On the nature of the horn, that is to say, the exfoliated product of the corium, and on the arrangement of horn tubules and inter-tubular horn, reference should be made to the work of NICKEL (1938, 1939). Nickel also refers to the three layers of the wall, relating their thickness to their value in accommodating to thrusts, and deals at length with the nature of the horn tubules and inter-tubular horn. Each tubule has a cortical and a medullary area and its growth is not dissimilar from that of hair. As growth continues the cells are pushed outward and downward and cornification proceeds. Of the horn tubule centre Nickel distinguishes three types; round, oval and wedge-shaped, this shaping is in part determined by the nature of the spiralling of the whole tube, which, in turn, is in keeping with mechanical requirements of stress. Here Nickel refers particularly to the steep spiral kind common in the middle layer (*Figures 14.7 and 14.8*).

We may thus summarize: the muscle tendons of the flexors and extensors which move the foot are well lubricated and angled for the purpose, the heel contacts the ground and impact is taken by the digital cushion and digital pad or frog, the lateral spread is taken on lateral cartilage (in the horse) and wall, and the spread from heel to toe is accompanied by increase of vertical thrust on the wall. The change of form of foot structures during movement is not great, but it is

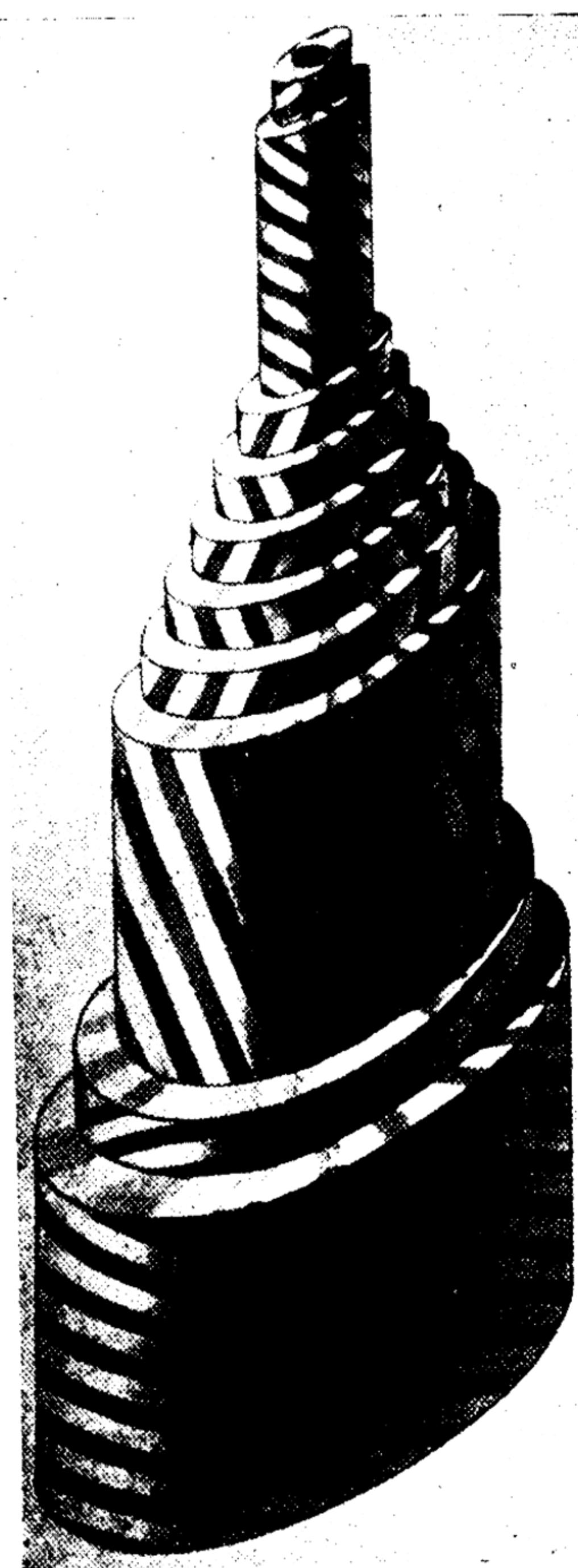


Figure 14.7

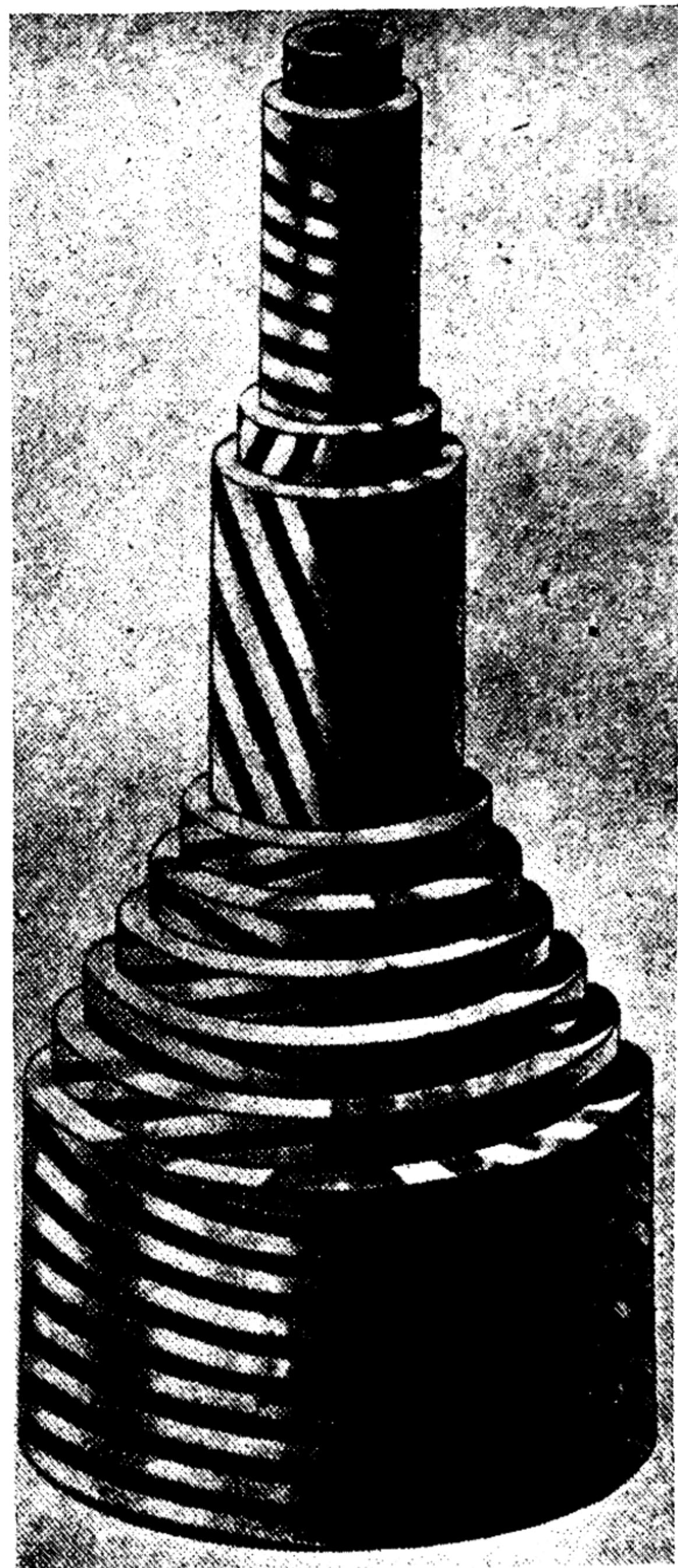


Figure 14.8

Figures 14.7 and 14.8. Diagrammatic representation of horn tubules: Figure 14.7 with mostly steep spirals, Figure 14.8 with a higher proportion of flat spirals. (From Nickel (1938), by courtesy *Morph. Jb.*)

reasonable to conclude, as did Sir Frederick Smith, that the hoof must contain structures which give and do not resist.

GAITS

In so far as the gait of an animal is the method of representing a locomotory act a consideration of gaits is necessary here, if only by way of being complementary to the remarks on the activity of units of the locomotory system. For pictorial representation, however, the reader is referred to the published works mentioned.

An animal at rest has to contend only with the problem of support, that is to say, in regard to the body as a whole, a vertical force counter-acting the power of gravity, but during movement the vertical force

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must be harmonized with the propulsive (horizontal) force, and it is the accommodation of these to fit the requirements of balance at the pace desired which determines the gait. There is also to be considered the lateral force, and the less this is the more effective is the forward progression; in speedy mammals body conformation is such that the lateral force is not great. In light of the above may be viewed determination of length of stride, placing of limbs, phase intervals and moments of suspension of limb or limbs in space. Another very important factor in this regard is movement of the head and neck. Although commonly used as an aid in the diagnosis of lameness it is remarkable how little attention has been paid to movement of the head and neck, or indeed of the vertebral column, when considering the normal gait.

The analysis of gaits is no new study; it is said that Borelli wrote on with which foot the horse commenced the walk*, and of late Simpson (1951) in his account has again brought to notice the dispute amongst ancient Egyptians as to whether a horse while trotting ever has four feet off the ground at once. It may well be that stimulus for the pursuit of this study in earlier centuries came from the belief that it would be as easy to study four legs in action as it was two, and that this misconception was responsible for the many inaccurate accounts and incorrect pictures which have appeared. However that may be it was only with the introduction of photography that really accurate information was obtained. Here again mention must be made of the pioneer work of Muybridge and his associates Stanford and Stillman, although it is only fair to say that many earlier observers had reached very near the complete truth without the aid of the camera. Interpretation of the slow paces was correct and the main fault when depicting the gallop was the representation of limb expansion during total suspension.

With the advance of ciné-photography it has been possible to examine many more frames per cycle than could Muybridge. But although analysis of consecutive frames has been of great value in estimating the activity of a given region at a given time, it is still customary, when analysing the gait, to select frames representing only a critical point, and it is, therefore, only through refinements of technique that much advance has been made beyond the days of Muybridge. The horse has been chosen by most authors as the example *par excellence*, and many works and pictorial representations are on record of the analysis of the gaits of this animal. No doubt influenced by the studies of their illustrious contemporary, Marey, the Frenchmen Goubaux and Barrier (1892) have, in their book on the exterior of the horse, devoted a section to the gait. They discuss

* This seemingly pointless question to which there can only be an arbitrarily chosen answer is of some importance when analysing gaits. It relates to the state of body equilibrium at the starting point.

generalities and specialities and introduce a modification of Marey's model for studying notations which they claim would represent the notation of any gait whatsoever. Further, they discuss defects in the gait which focuses attention on the close connection which exists between the study of gaits and the study of lameness. This same point has been mentioned by Smith (1912) in his analysis of the paces. Smith considers the walk a most important and instructive pace and draws attention to the fact that few horses walk well without education—which prevents stumbling. His notation* of the walk shows the triangle of support alternating with a two-footfall phase.

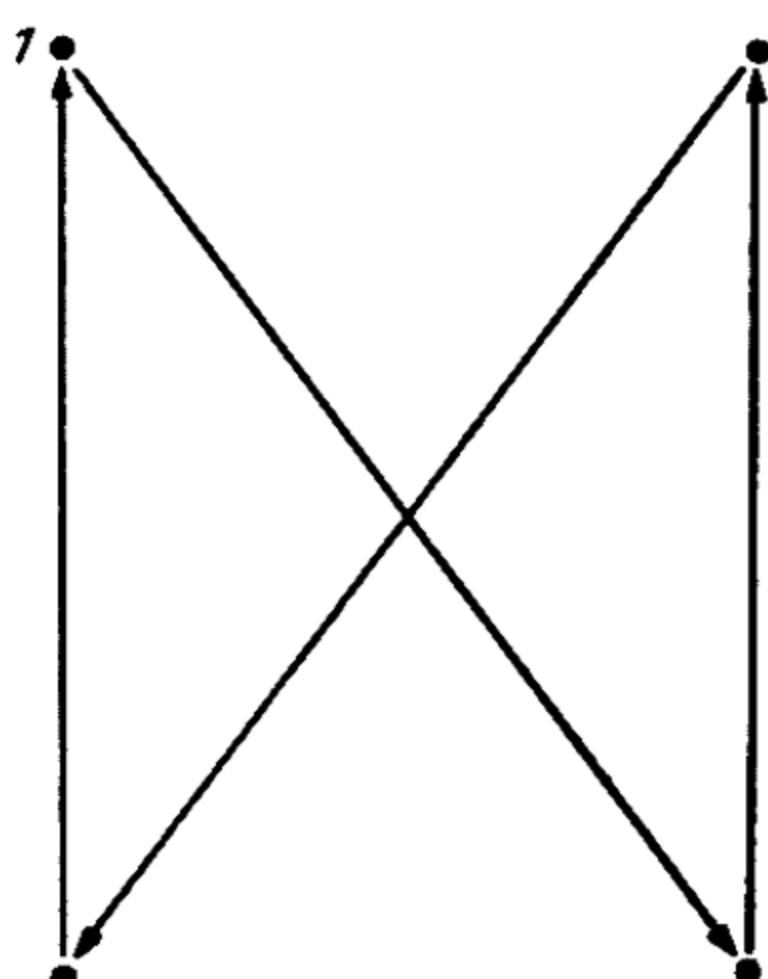


Figure 14.9. Drawing to indicate a method of representing order of footfall at the walk, commencing with descent of the left fore foot (1).

The other regular pace according to Smith, the trot, he demonstrates as two diagonally opposite feet on the ground, then all in the air, and then the opposite diagonals on the ground. The canter, that most comfortable of paces from the point of view of the rider, he regards as essentially a three-legged support movement as with the walk. Following such a support phase two lateral legs are in contact with the ground, the hind is then picked up and the fore leg propels the body into the air, the first leg to contact the ground after the spring is the diagonally opposite hind. The gallop may be a transverse or rotatory movement, in this Smith quotes Muybridge. The horse employs the transverse, the dog the rotatory action, and one is tempted to relate this to the differing methods of back movement in these two type species, especially as with the speedy dog all limbs are off the ground for two periods during the cycle. The most interesting feature of the gallop is possibly the 'collection' of the pairs, be it under the body or in the extended or semi-extended position. This would seem to be an attribute of speed.

It is well known that vertebrates with long legs make less use of body bending from side to side than do short-legged animals and

* Smith's method of representing notations is clear if unorthodox: a triangular-shaped line figure represents the animal, the base is rounded and indicates the hind quarters, the apex the head. Spots on the figure demonstrate legs on the ground at any one moment.

A complete record of a notation will indicate limbs on the ground and limbs in the air; if it is required only to represent the order of footfall, of value in recalling sound as well as sight of the descending foot, a simple dot and arrow drawing will suffice (Figure 14.9).

'belly-crawlers'. The domesticated species do demonstrate a slight lateral roll which increases the stride, but otherwise bending movements are restricted to those in the sagittal plane. In a review of vertebrate locomotion DE LA CROIX (1936) refers to these tractive and propulsive methods of progression and then discusses the gaits of mammals at different paces with particular reference to the horse. He explains that it is necessary to consider the step as being capable of division into six periods, three by a normal pendulum—the centre of movement being the hip or shoulder—and three by an inverted pendulum—the centre of movement being the point of contact with the ground. This is in keeping with the periods of the two phases of the stride advanced earlier in this chapter. In addition the possibility of pauses between any two periods must be considered, the existence and duration of which are associated with the number of feet on the ground at any one time. At the gallop de la Croix draws attention to what he terms the centrifugal and centripetal attitudes, *i.e.* legs askance and under the body at different stages of the cycle.

Most writers would seem to agree by implication if not by word that analysis of slower paces yields more detailed information than does analysis of fast paces, at least from the mechanical point of view. Thus Gray (1944), in discussing the theory of the mechanics of the walk of the tetrapod, relates the sequence of the step to the requirements of stability. Assuming vertical and lateral oscillations of the body to be at a minimum he states that co-ordination of limb effort should be such that the resultant propulsive force acting on the body should always be a horizontal force acting through the centre of gravity of the body. Gray continues that in order that these conditions should be completely fulfilled in respect to vertical disturbances two features are necessary: (1) not less than three feet should be on the ground at any one instant, and (2) no foot can be left off the ground unless the centre of gravity of the body lies within the triangle of the other three feet. Reviewing six possible sequences which could occur if all limbs stepped with equal frequency and length of stride, he indicates that only if the feet be moved in diagonal pattern is full stability obtained. The horse at the walk adopts the diagonal pattern of progression, and the fact that two-feet support, at times of a lateral nature, occurs during the cycle does not detract from the value of this mechanical analysis, especially as it is known that at a slow walk a two-support phase is immediately stabilized by a three-support phase and that Gray is only considering slow paces. To these theoretical observations can be added those of Manter (1938) who relates whole body movement to the alternate braking and propulsive efforts of individual limbs, and considers the vertical, horizontal and lateral forces at work during the walk of the cat. It is felt that Manter's observations have a direct application to the study of movement of

other four-legged species, in particular those which relate to co-ordinating factors of whole body activity and those concerned with movement of the body on its longitudinal axis.

Howell (1944) also reviews the gaits in his treatise on speed in animals. As this work is essentially concerned with speed, and at that in many kinds of animals, he is more able than most authors to indicate how slight differences in pace will change the sequence of footfall of the same gait and greater differences in pace the gait itself. Quite obviously speed is the controlling factor of the kind of gait adopted. Further, although Howell chooses the horse as a basic example, illustrated by most excellent line drawings of ciné films, he introduces records of other animals in movement to lend support to his suggestion of similarities and dissimilarities of gait. He works on the assumption that it is best to have a formula on which all gaits can be based. Thus he states each gait has eight important periods: one for each of the four individual footfalls and one for each time each foot is suspended. If two footfalls occur or two feet are suspended at the same instant the series of eight will be shortened or telescoped. For example in the trot the formula is shortened from eight to four as the feet are synchronized in pairs. It is pointed out that there are dangers to be avoided when using this method, as indeed there are in using any method which has been advanced. The intervals between the periods or phases must not be considered as equal, and there is a difficulty in assessing the precise moment at which weight is removed from, or received by, a foot, that is to say when it leaves or meets the ground. He next subdivides gaits into three main groups: the walk, trot and gallop, of which the first two are symmetrical, the gallop asymmetrical. Other than the question of symmetry of the support pattern there are differences in the interval between footfalls and in the method of bending of the back, in this sense plane not degree of bending. There is little, if any, vertical bending of the back in the slower symmetrical gaits, that is to say in the sagittal plane, whereas in the gallop it is a pronounced feature. The degree and areas involved in vertical bending of the back at the gallop are, however, a matter of species peculiarity, not a matter of symmetry. When discussing the symmetrical trot, Howell introduces another interesting point. If fore limbs are shorter than hind, the length of time a fore limb is suspended must be greater than the diagonal opposite hind. This he associates with the greater vertical deflection in the dorsal direction of the fore quarters and in another place he discusses differences in limb length in connection with the tendency towards bipedalism in those stocks adopting a fast symmetrical gait.

It is tempo which Howell features when discussing the walk and it is noticed that his analysis shows that with increase of walking-pace so the frequency of two-legged support increases, nevertheless,

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periods of instability in the sense advanced by Gray are never very prolonged. At the gallop Howell refers to the value of the combined action of hind limbs and body and the use of the powerful neck muscles, features which have already been mentioned here. There is no doubt, as he states, that movement of the head and neck adds greatly to the value of the rhythm and movement of the fore limbs; in this he instances the action of the brachiocephalic muscle. One feels that it is the winding up and unwinding of quarters and neck on the body which is of value to speed at the gallop and that the suspension period is merely a reflection of this activity. At the gallop and the canter (which is really a slower tempo of the gallop with a slightly different formula) there is typically one period of body suspension in each cycle. Many writers have confirmed that with the horse at the gallop it is a fore foot which is the last to leave the ground before the period of suspension when all four legs are under the body, the so-called centripetal position. With 'leaping' animals of lighter weight than the horse, but of fair speed, a hind foot is the last to leave the ground and the suspension period is that with legs extended (centrifugal position). Heavy and slow dogs adopt the same suspension pattern as the horse, but lighter and fast animals like the greyhound have two periods of suspension, one following the hind limb propulsion or take-off and one the fore limb, so that in both the fully extended and fully flexed position the animal is in the air. It would seem, therefore, that the matter of body suspension is related to relative weight and general body conformation as much as it is to speed.

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REPRODUCTION

CHAPTER 15

EGG PRODUCTION AND FERTILITY IN POULTRY

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As MIGHT be expected in view of the dominant interest in endocrinology during the past several decades, much of the work on the reproductive physiology of the avian female has had its origins in this field. In avian as well as in mammalian reproduction, ovarian-pituitary relationships (which in some respects should perhaps now read ovarian-neural-pituitary relationships) have come to occupy a place of central importance. A main objective of the following discussion is to examine these relationships as they are expressed in the processes of egg production by the domestic fowl.

A large part of this chapter is devoted to an exposition of the cycle in egg production, *i.e.* the typically short term cycle that finds its simplest expression in two well recognized observations: the lay of eggs at later hours of the day when eggs are laid on two or more days consecutively to form a sequence (or clutch), and a *single* day of 'missed' lay between such sequences (or clutches). In a sense, some concept of a cycle is implied in any attempt to explain why a hen does not lay an egg on a single day (typically) between sequences; or, to make the same point in another way, to explain why the hen does not lay her eggs at equal intervals around the clock, at greater or lesser intervals, ideally uniform, in accord with her 'rate of production'. At first sight these may seem trivial objectives, but in the end they come to involve fundamental relationships between the ovary, the hypophysis, and the central nervous system. At this remote level 'the cycle' turns out to be a most convenient frame of reference in formulating these relationships, serving much as does the more familiar oestrous cycle of the spontaneously ovulating mammal.

Limitation of this essay to some of the more basic and general aspects of egg production would perhaps be unwarranted were it not for the appearance, during 1954, of Sturkie's *Avian Physiology*. In this volume, STURKIE has devoted all or considerable parts of four chapters to what, in substance, becomes a résumé of recent progress in the

physiology of egg production. There seemed little point, certainly, in undertaking here a repetition of the task carried out so well by Sturkie.

In addition, fertility and incubation have been reviewed in a volume edited by TAYLOR in 1949, and incubation was reviewed most thoroughly by LANDAUER as late as 1951. The avian egg, its composition and properties is the subject of a volume by ROMANOFF and ROMANOFF (1949). The first chapter of this volume affords a good introduction to laying behaviour in birds, and more specifically in the fowl. The effects of light on reproductive behaviour of birds as well as mammals are discussed in an earlier chapter in the present volumes (YEATES, 1954).

The author wishes to thank Dr. C. S. SHAFFNER of the Poultry Department, University of Maryland, and Dr. M. W. OLSEN of this Laboratory for their gracious assistance in preparation of the last section of this chapter.

THE ORGANS AND PROCESSES OF REPRODUCTION IN THE FOWL

The reproductive system of the fowl consists typically of a single ovary, which is the primary organ, and the accessory organ, the oviduct. The ovary produces and matures the female reproductive cells, or ova; it also secretes endocrines—oestrogen, androgen and possibly progestin—which are vital in regulating the reproductive processes. The avian ovum differs from that of the mammal mainly in that it carries a relatively enormous mass of yolk, and the bird's ovum is often referred to as the yolk. When the mature ovum is dropped from the ovary (ovulation) it enters or is picked up by the oviduct. Here it is fertilized, the albumen or egg white is secreted, the shell membranes and shell are formed, and as a final function of the oviduct, the egg is laid (oviposition). In wild birds, reproduction also includes the important process of brooding, or incubating, the egg (or clutch of eggs), but this aspect of reproduction is of incidental concern here.

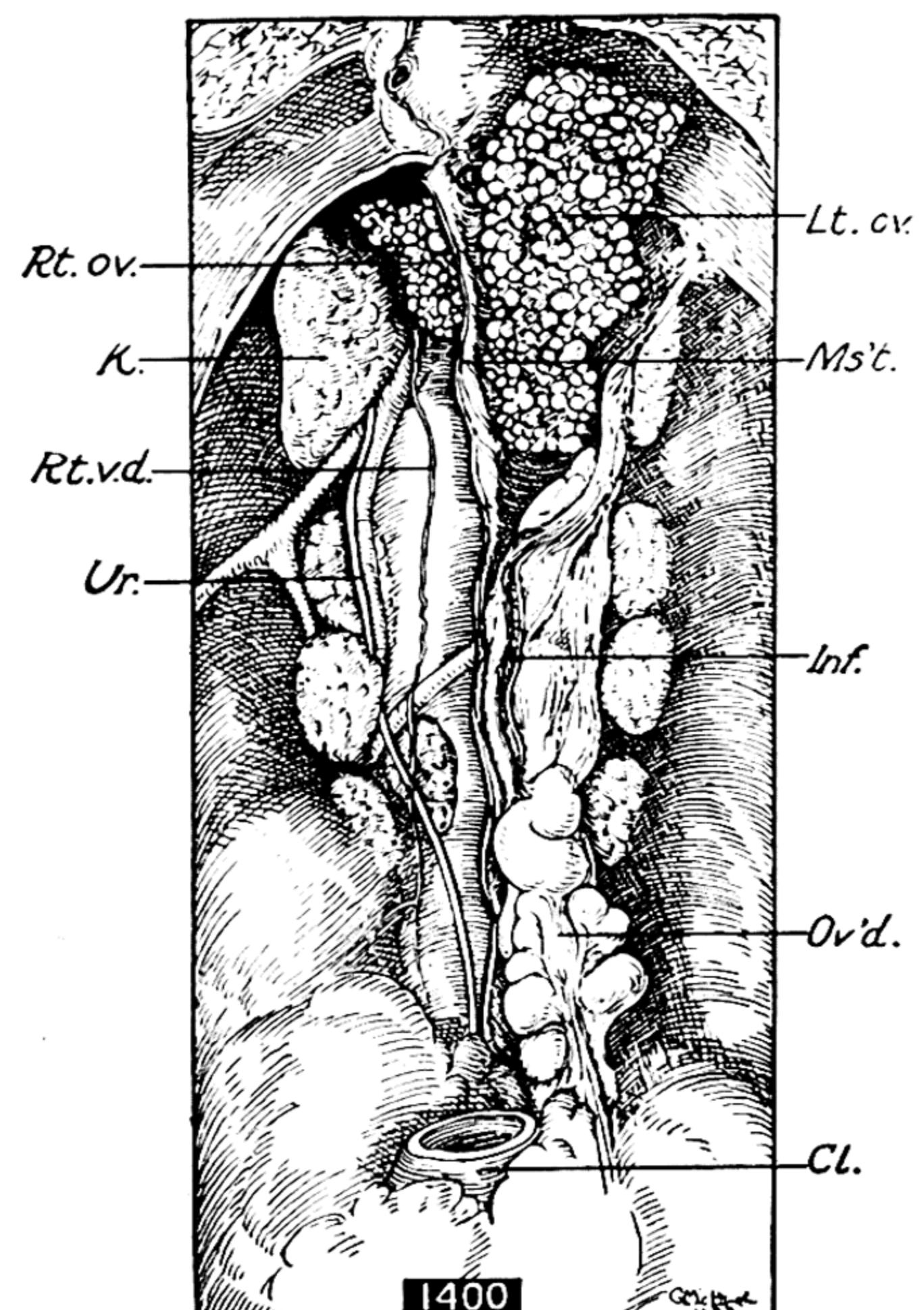
THE OVARY AND ITS FUNCTIONS

Only a single functional ovary, the left, is normally found in the domestic fowl. Both a right and left ovary appear in early stages of embryological development, but growth of the right gonad ceases between the 7th and 9th day of incubation; a rudiment nevertheless persists (DOMM, 1939). Occasionally, the right ovary (and oviduct) may develop in the fowl (CREW, 1931; QUINN, BURROWS and McNALLY 1939, and others cited by Sturkie, 1954). Upon removal of the left ovary, the right gonad hypertrophies, becoming a testis-like organ (see Domm, 1939).

EGG PRODUCTION AND FERTILITY IN POULTRY

The left ovary in the chick at, and for some time after, hatching, is seen as a small flat, sheet-like mass, in close association with the ventral surface of the left iliac vein and vena cava. As a rule it extends over the median border of the left adrenal gland, and may cover much of this gland. At this stage the ovary is made up of an outer portion, the cortex, which contains numerous small ova, and an inner mass, the medulla. The ova are surrounded by cells which form, in varying stages of development, the follicle (see BENOIT, 1950, and Romanoff and Romanoff, 1949).

Figure 15.1. The urino-genital system of a normal adult Leghorn hen preceding the first laying cycle. Note the small right ovary. Right ovaries ranging from normal size to such as are barely visible occur in less than 5 per cent of adult brown Leghorn hens. Cl., cloaca; Inf., infundibulum; K., kidney; Lt. ov., left ovary; Ms't., mesentery; Ov'd., oviduct; Rt. ov., right ovary; Rt. v.d., right vas deferens; Ur., ureter. (From Domm (1939), by courtesy Williams & Wilkins.)



Long before the onset of laying, large numbers of follicles are easily recognizable on the surface of the ovary (*Figure 15.1*). These form a graded series, though the vast proportion of available follicles (and oocytes) remain microscopic. At about 8 or 10 days before the onset of laying, the rate of growth of the larger follicles is greatly increased. The gradation in size of ova (or follicles) is maintained, so that just before ovulation we have essentially the ovary of the immature bird plus some five to eight follicles ranging in weight from a small fraction of a gramme to some 16 grammes. The tremendous increase in weight of the ovary during this relatively brief span of time is therefore due mainly to increase in weight of these few, rapidly growing follicles. Substantially the same relationships are seen in the ovary of the regularly laying hen (*Figure 15.2*), although total weight

of the ovary may increase even further with increasing size of the follicle at ovulation.

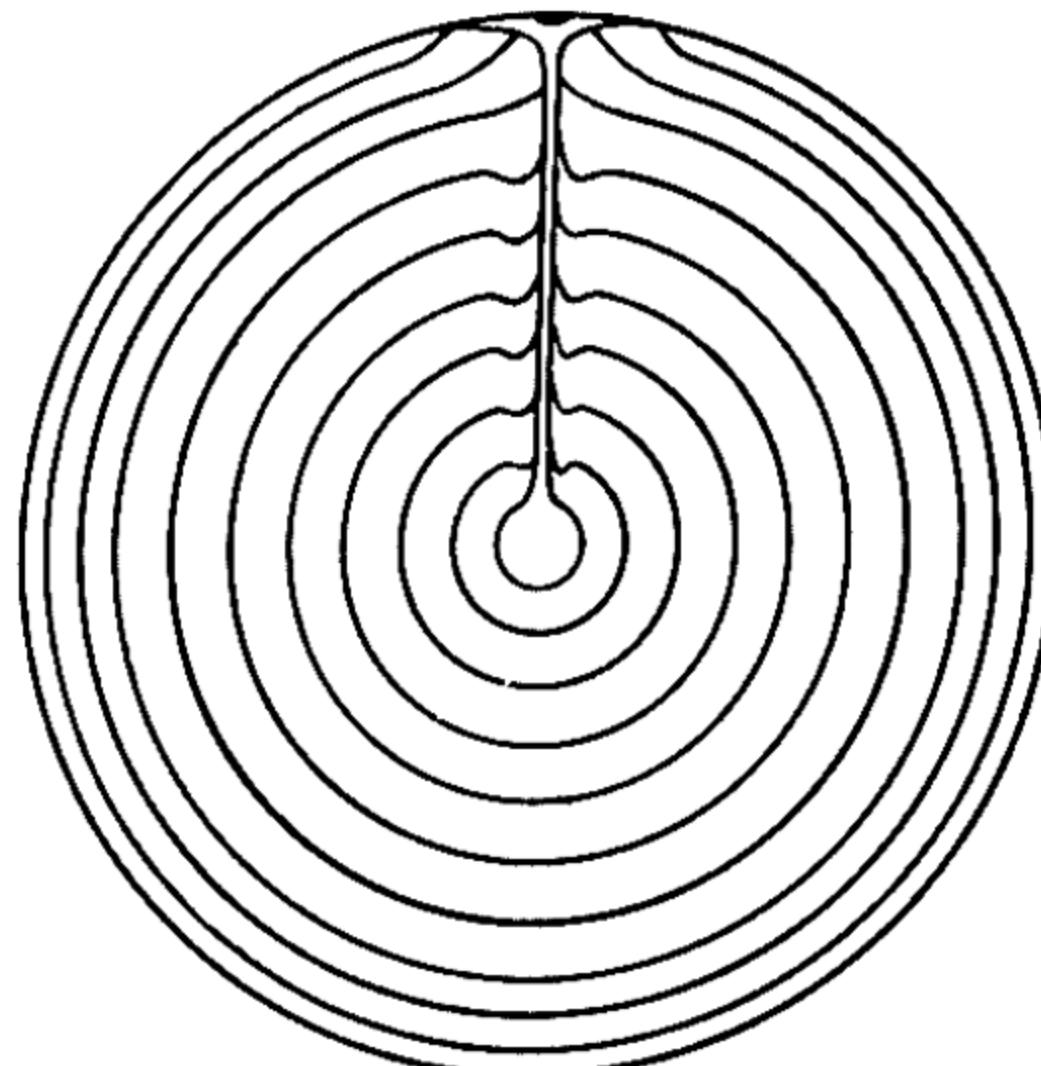


Figure 15.2. Left, the ovary of a hen coming into production following a pause. Right, the ovary of a regularly laying hen; note the ruptured follicle.

Rate of ovum growth

The rate of growth of the smaller ova is difficult to measure; it is certainly very slow (MARZA and MARZA, 1935). With onset of the final period of rapid growth, rates of growth can be determined with considerable accuracy. Actually, rates of growth during this period refer to rate of yolk deposition, since the ovum proper (the germinal elements) do not increase in size (OLSEN, 1942).

Figure 15.3. Diagram of the yolk of an egg of hen No. 3925, giving the position of dye bands resulting from nine 24-hour interval injections. Each concentric ring indicates the size of the yolk at the time of the injection. The latebra is in the centre, and its neck joins the germinal disc. (From Warren and Conrad (1939), by courtesy *J. agric. Res.*)

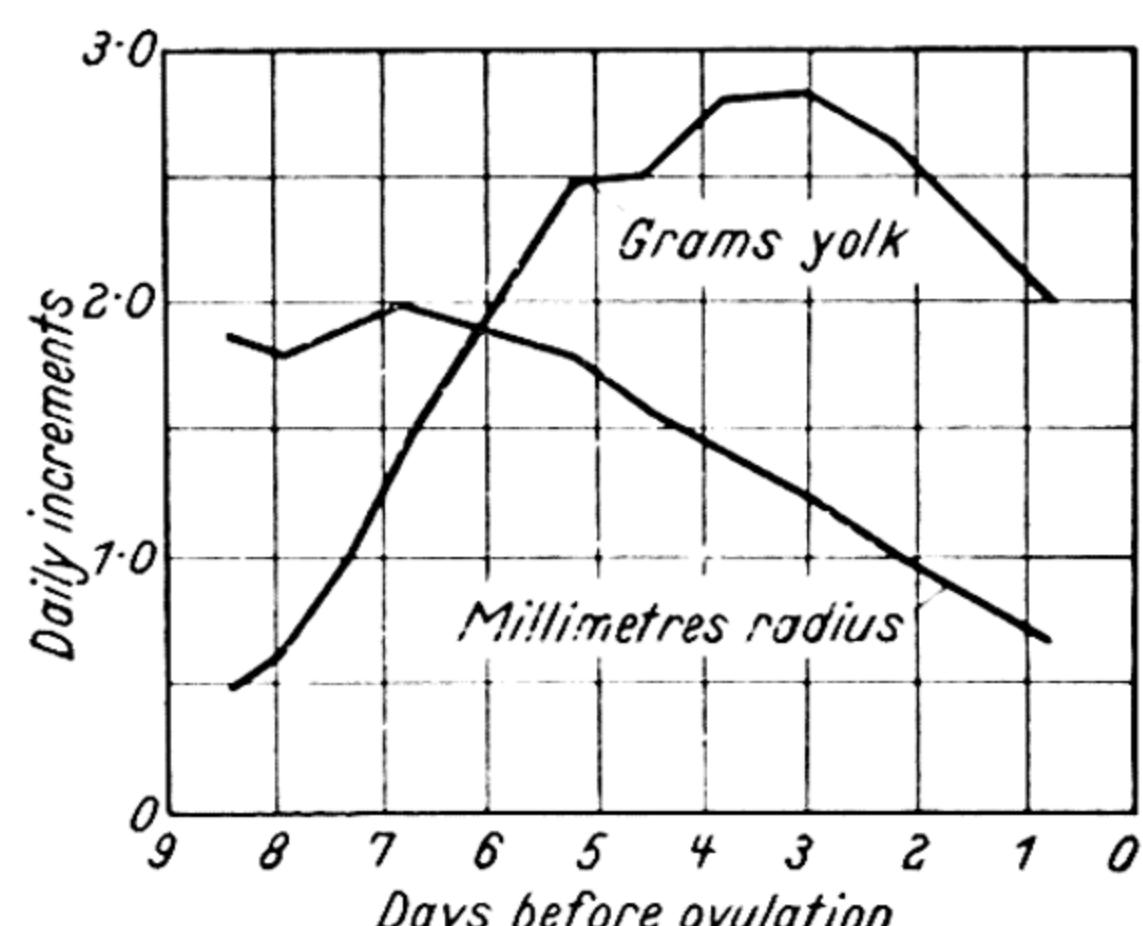


STIEVE (1918) estimated growth curves for the hen's ova from weights of ova removed from the ovaries of regularly laying hens, an approach which might still prove useful for some purposes. RIDDLE (1911) fed fat soluble dyes to laying hens at known times, and estimated rate of yolk deposition from the separation of the bands of dye found in the yolk of the hard boiled egg. CONRAD and WARREN (1939) and WARREN and CONRAD (1939) greatly increased the precision of Riddle's method by injecting the dye intravenously. The diameters of the yolk at the times of successive 24-hour injections are shown diagrammatically in Figure 15.3.

A more instructive analysis of yolk deposition during the 9 days before ovulation may be gained from the relations shown in Figure 15.4.

The mass of yolk laid down daily is seen to increase from the ninth to the third or fourth day before ovulation, after which it decreases until ovulation. Daily radial increments, however, appear to be about constant from the ninth to the seventh days before ovulation; from the seventh day onwards, daily radial increments decrease progressively, and one day before ovulation are only about a third of the maximum recorded on the seventh day before ovulation. Since the daily radial increment of yolk deposition is a measure of the quantity passing through a unit of the follicle's surface area, it is clear that the capacity of the follicle to lay down yolk decreases from the seventh day onwards.

Figure 15.4. Yolk growth curve showing the daily increments of radius and weight in 367 eggs. (From Warren and Conrad (1939), by courtesy *J. agric. Res.*)



According to Warren and Conrad, the decreasing rate of yolk deposition seen in *Figure 15.4* probably continues until ovulation; no evidence was found by these authors of any 'last minute' increase in rate with the approach of time of ovulation.

Warren and Conrad showed also that rate of yolk deposition was not related to rate of laying or to prospective place of the ovum in the sequence (or clutch) of eggs. This last point is of particular interest, for it indicates that yolks are not segregated into 'clutches' by characteristic rates of growth.

The alternate 'white' and yellow bands frequently seen in the hard boiled yolk of the hen's egg were shown by Riddle (1911) to be laid down each 24 hours. Riddle believed the varying colour of yolk to indicate a diurnal rhythm in metabolic rates. Conrad and Warren (1939) observed, however, that these bands were not found in eggs from hens fed a uniform all mash ration *ad libitum*. This observation led Conrad and Warren to determine rates of yolk deposition during day and night hours. A very slight decrease (approx. 3 %), of questionable significance, was found to occur during early morning hours. This difference was believed to be too small to signify any appreciable change in rate of yolk metabolism. Conrad and Warren showed also that the bands of alternating yolk colour could be produced by providing, at given times of day, feeds containing sufficient xanthophyll to cause a periodic increase in concentration of this pigment in the blood stream.

Hormonal factors in follicular development

Oogenesis and very early development of the follicle in the bird, as in mammals, probably proceeds independently of pituitary control (see discussion by HISAW, 1947). Just how far follicular development may proceed in birds in the absence of hypophysial hormones is uncertain. HILL and PARKES (1934) found no follicles of more than 1 or 2 mm diameter in a hen following hypophysectomy. A rapid regression of all large follicles occurs following hypophysectomy. The pituitary gonadotrophins are therefore as essential for maintenance of the ovarian follicle as for its growth and development.

The rapid follicular development seen in the hen approaching sexual maturity and maintained in the laying hen, is dependent upon gonadotrophins from the hypophysis (BRENEMAN, 1954, for review). As in mammals, the follicle stimulating hormone (FSH) appears to be



Figure 15.5. The ovary of a hen treated for 12 days with a follicle stimulating preparation from swine pituitaries; the preparation was known to contain also some luteinizing hormone.

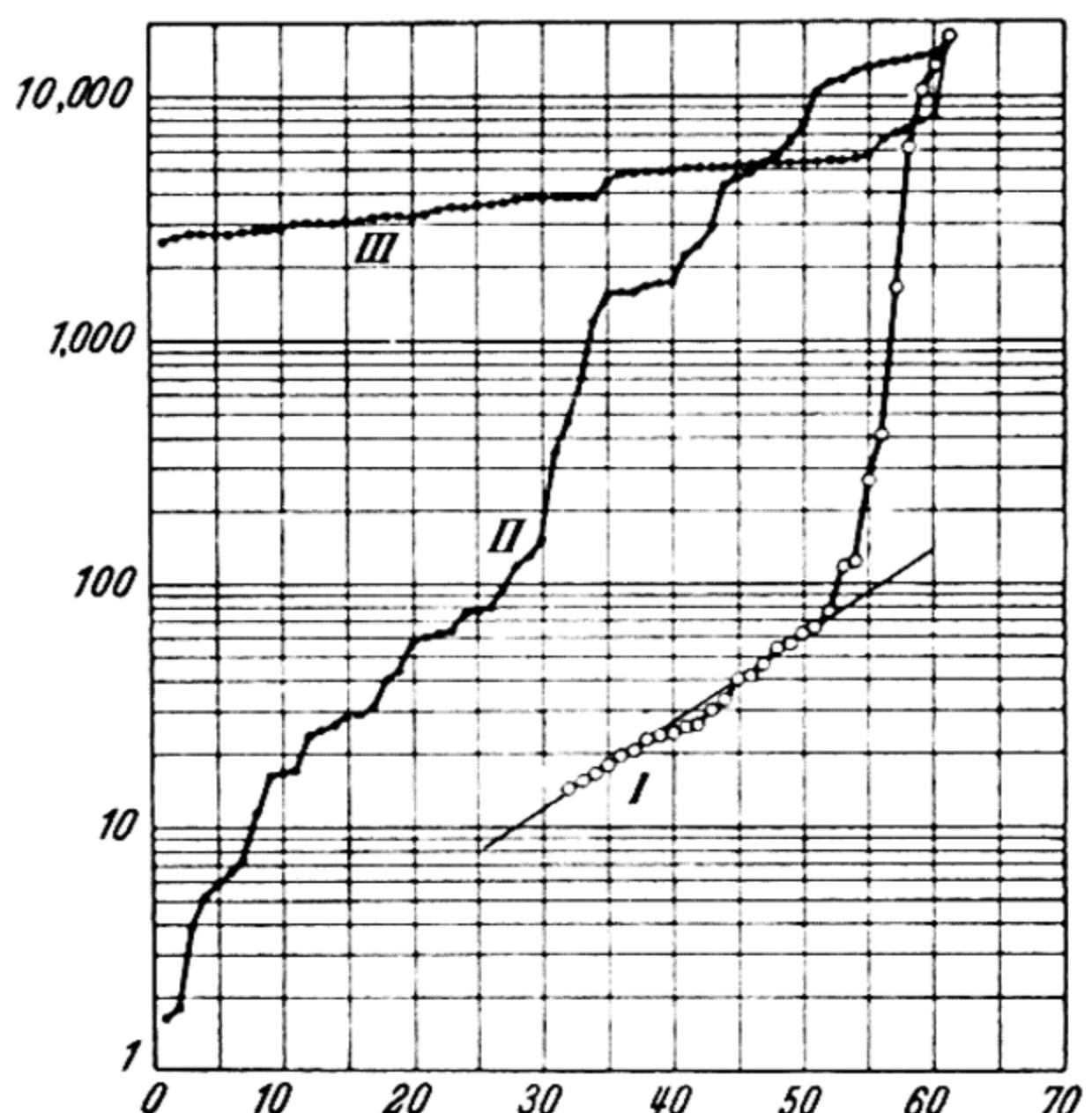
the gonadotrophin chiefly responsible, but the luteinizing hormone (LH) is probably also involved in the normal process (HISAW, 1947; NALBANDOV, 1953a). In the laying hen, preparations rich in FSH cause extensive follicular growth (BATES, LAHR and RIDDLE, 1935; FRAPS and RILEY, 1942; PHILLIPS, 1943; NALBANDOV and CARD, 1946). An example of such stimulation may be seen in *Figure 15.5*; none of the follicles in this ovary was greater than maximal normal size, but many follicles were approaching full size.

Follicle stimulating preparations of anterior pituitary origin (containing some LH also), as well as pregnant mares' serum (PMS), result in cessation of ovulation within a few days; some of the larger follicles carried by a stimulated ovary represent therefore only the accumulation of unovulated follicles. However, the distribution of follicles in normal and stimulated ovaries (*Figure 15.6*) makes it plain that many follicles are caused to grow rapidly, from a relatively small size, by the stimulating hormone (in this case PMS).

While the ovary of the laying hen is highly responsive to FSH preparations, the immature ovary—as Nalbandov (1953a) has pointed out—remains refractory to such preparations until a short time before the normal onset of sexual maturity (Nalbandov and Card, 1946).

Moreover, it has proven impossible to maintain indefinitely the ovary of hypophysectomized hens by means of gonadotrophin injections (Nalbandov, 1953a), although preparations of avian origin seem more promising in this respect than do similar preparations of mammalian origin. According to NALBANDOV, MEYER and McSHAN (1951), LH of avian origin may differ from that of mammals, or a third gonadotrophic hormone may be present in fowl pituitaries. The mechanism of action of the postulated third gonadotrophin is believed to exist also in laying hens (Nalbandov, 1953a). The gonadotrophic activity of

Figure 15.6. The effect of pregnant mares' serum (PMS) on growth of ovarian follicles. Each curve represents the weights of follicles (ordinates) ranged in order of increasing weights (abscissae). Curve I: from the ovary of a normally laying hen. Curve II: from the ovary of a laying hen after 13 days injection of PMS (80 R.U./kg. daily). Curve III: from the ovary of a laying hen receiving PMS for 17 days (80 R.U./kg. daily).



blood serum from non-laying hens was found by BAILEY and PHILLIPS (1952) to be higher than that from laying hens. The source of the difference was not identified. It is obvious that we have much to learn respecting the conditions, endocrine and other, under which the ovary develops, and is maintained, in the actively laying hen.

OVULATION

The process by which the ovarian follicle ruptures and simultaneously discharges the ovum (or yolk) is known as ovulation. Throughout the period of rapid growth, the future site of follicular rupture, the stigma, is recognizable as a macroscopically avascular band extending roughly over half the circumference of the follicle, and always in the hemisphere apposed to the follicular stalk (*Figure 15.7*). Actually, the region of the stigma is not avascular, but is traversed by small arteries and veins (KRAUS, 1947; NALBANDOV and JAMES, 1949). Some degree of vascularity certainly is to be expected, since ovulation (or follicular rupture) is caused by a hormone circulating in the blood stream.

The process of ovulation was observed long ago in the pigeon by BARTELMEZ (1912). Subsequently, WARREN and SCOTT (1934, 1935a)

and PHILLIPS and WARREN (1937) reported on the course of ovulation as seen in celiotomized hens. They also observed ovulation of a few follicles excised an hour or so before expected ovulation. OLSEN and NEHER (1948) found that follicles excised about an hour before expected ovulation and placed in a little modified Ringer's solution at a temperature of 107° F. proceed to ovulate, apparently normally (see also NEHER, OLSEN and FRAPS, 1950).



Figure 15.7. Ovary of a laying hen, treated to show the stigma of maturing follicles.

Shortly before ovulation, the stigma appears to widen, due to obliteration or blurring of the numerous small blood vessels extending toward or into the region. Phillips and Warren (1937) found that tension artificially applied to a nearly mature follicle caused a similar obliteration of vessels, and they state that 'prolonged tension of the muscle fibres in the follicular membrane' may be one of the immediate causes of follicular rupture. While some degree of tension—or elasticity—in the follicular walls is an essential condition for expulsion of the ovum (or yolk), it seems doubtful that it plays more than a secondary role in rupture of the follicle, as Kraus (1947) concluded.

The act of rupture in the follicular walls proceeds very rapidly. In some instances, Phillips and Warren noted that an inner layer of the walls ruptured first, resulting in a bulge in the outer walls. Usually this bulge appeared in one pole of the stigma. Once rupture is completed at this point, it extends rapidly to the opposite pole, freeing the yolk almost immediately. The walls of the follicle along the line of rupture are clean, and the edges are blunt; there is no evidence of 'tearing' of tissue as might be expected if rupture occurred before the site of rupture was well differentiated. Kraus (1947) concluded, on

the basis of similar observations, that the main factor in follicular rupture was the induction of 'regressive morphological changes' by hormone action in the stigma, the effects of other factors being of minor, if essential, importance.

The hormone acting on the follicle to cause its rupture is a gonadotrophin from the anterior pituitary body. This ovulation-inducing hormone (OIH) is probably the luteinizing hormone (LH), as it is also in mammals. Release of OIH into the blood stream is believed to take place some 6-8 hours before the ensuing ovulation, though evidence on this point is not conclusive. The hormonal control of ovulation, and of the mechanism which in turn controls the release of gonadotrophin for ovulation, are discussed in a later section.

The ruptured follicle

Following ovulation, the follicle walls form a loosely folded structure appropriately described as the calyx, but more commonly known as the ruptured follicle (*Figure 15.2*). In the hen, the ruptured follicle weighs some 0.3 to 0.5 gramme immediately following ovulation. It undergoes rapid involution, decreasing to about half its initial weight in 30-35 hours (*Figure 15.8*). As can be seen in *Figure 15.8*, the rate of regression (in weight) is proportional to the mass at any instant over a considerable range. The ruptured follicle plays an important role in the timing of oviposition (ROTHCHILD and FRAPS, 1944a) a function which however appears to be shared with the ovulating follicle in timing of all except the terminal oviposition of a sequence (or clutch). The action of the ruptured follicle may therefore be more profitably examined in connection with the oviducal term and the mechanism of oviposition.

Maturation of the ovum

Maturation changes in the ovum of the fowl or turkey, as in birds generally, include dissolution of the well defined germinal vesicle and extrusion of the first polar body (Olsen, 1942; OLSEN and FRAPS, 1944). These changes, together with others involved in preparation of the ovum for fertilization, have long been known to be completed by the time of ovulation. More recently, it was shown that maturation changes in the hen's ovum were initiated only following release of gonadotrophin for ovulation of the follicle containing that ovum (OLSEN and FRAPS, 1950). Microscopically visible changes were apparent by about 4.5 hours before ovulation, and were completed well before ovulation occurred. The timing of events with reference to estimated time of release of luteinizing hormone (for ovulation) is shown in *Figure 15.9*. When ovulation was induced prematurely by the injection of a pituitary preparation, maturation changes also occurred prematurely, and in correspondence with time of injection of

REPRODUCTION

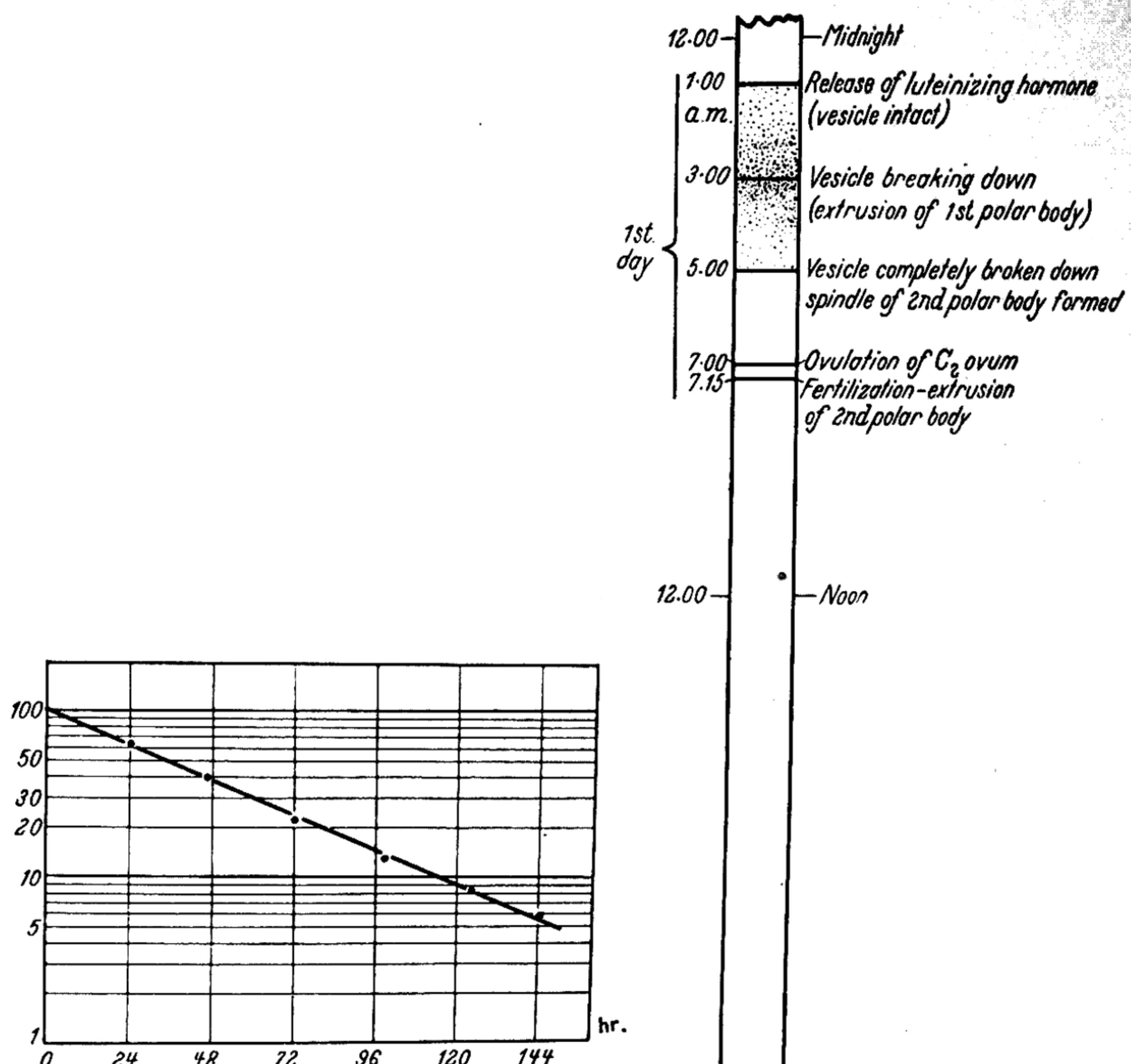


Figure 15.8. The rate of loss in weight of the ruptured follicle as a function of its age (i.e., time in hours from rupture).

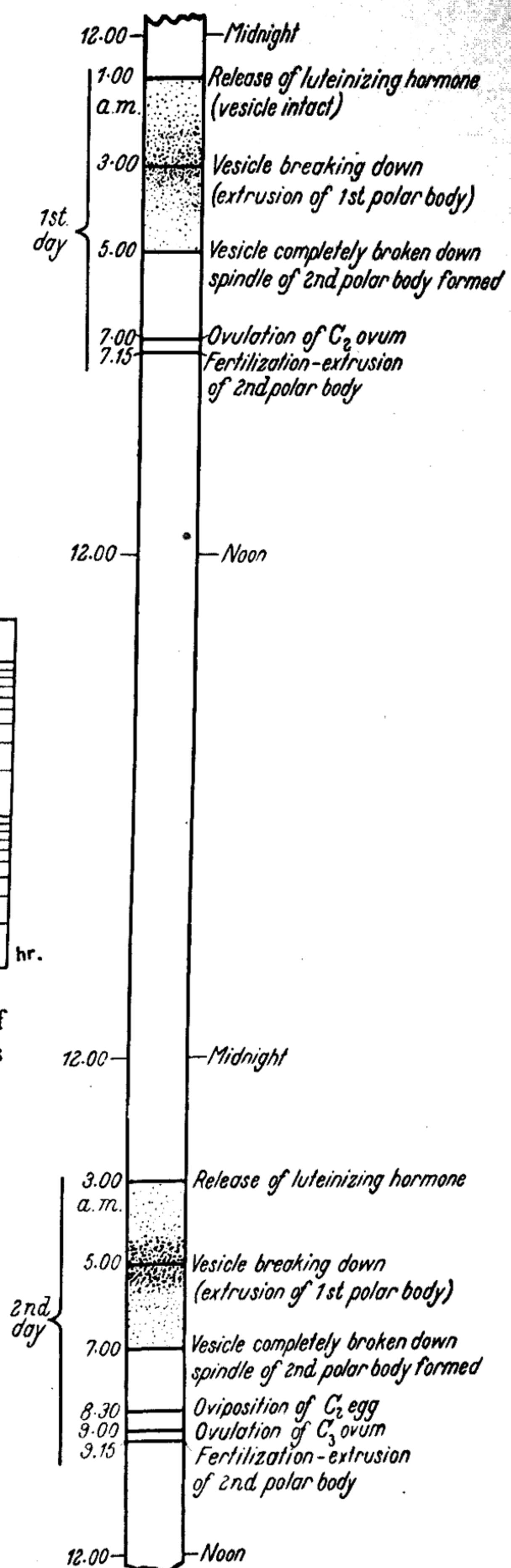


Figure 15.9. Time schedule of the sequence of events occurring in the final stages of maturation of the second (C_2) and third (C_3) ova in the hen's sequence. (From Olsen and Fraps (1950), by courtesy *J. exp. Zool.*)

EGG PRODUCTION AND FERTILITY IN POULTRY

the ovulation-inducing hormone. Eggs from such prematurely ovulated ova are fertilized and develop like the normal (NEHER and FRAPS, 1946).

It was of some interest to find that the germinal vesicles of follicles from ovaries stimulated by PMS resembled those of the normal hen before release of ovulation-inducing hormone. Even though some of the PMS treated follicles normally would have ovulated, and their ova matured, 5 or 6 days before they were observed, no maturation changes occurred in absence of the ovulation-inducing release from the pituitary.

Maturation of the hen's ovum is similar to the mammalian ovum in its dependence upon processes associated with the release and action of LH for ovulation; but in the hen there is no freshly grown complement of ova to be acted on by successive releases of LH, as in the mammal. An ovum which fails to respond, by maturation changes, to a given LH release may do so promptly 24 hours later; it does so, however, only if its follicle has become capable of responding to the same release of LH by ovulation. The processes of follicular maturation may make the ovum responsive directly to the release of LH (for example, by altering characteristics of the vitelline membrane); alternatively, the mature (ovulating) follicle may produce some hormone or other substance, under the influence of LH, which in turn brings about maturation of the ovum. A resolution of the problem posed by these alternatives is not possible at this time.

THE OVIDUCT AND ITS FUNCTIONS

Like the ovaries, two Müllerian ducts, or oviducts, appear in the female embryo. The right duct of the female commonly undergoes involution from about the eighth day, but a rudiment persists throughout life (Domm, 1939). Not infrequently involution is incomplete or fails to occur, and two normal or nearly normal oviducts may occasionally develop (Domm, 1939). Usually, however, only the left oviduct develops and becomes functional.

Before onset of the period of rapid follicular growth, the oviduct is seen as a threadlike, unconvoluted organ some 8–10 cm in length (*Figure 15.1*). More or less coincidentally with onset of the period of rapid follicular growth, the oviduct also undergoes a rapid growth, becoming within a short time a highly convoluted, fairly massive structure some 50–60 cm in length (*Figure 15.10*). The source of this sudden growth (and development) is oestrogen from the rapidly growing ovary and its follicles. JUHN and GUSTAVSON (1930) first demonstrated that this phase of accelerated oviducal growth could be simulated in the immature female by oestrogen, a finding which has since been confirmed under a great variety of conditions (see Sturkie, 1954).

While oestrogen seems to be the only stimulus required for maximal growth of the oviduct, another steroid, possibly progesterone or a

progesterone-like steroid (a progestin), is apparently necessary for its complete function. Thus the formation of avidin, the anti-biotin factor found in egg white, may be induced regularly in the oviducts of immature birds by the administration of progesterone and similar steroids following pretreatment with oestrogen, but only rarely by oestrogen alone (HERTZ, FRAPS and SEBRELL, 1943). Avidin was not found in the oviducts of non-laying hens, but always appeared with

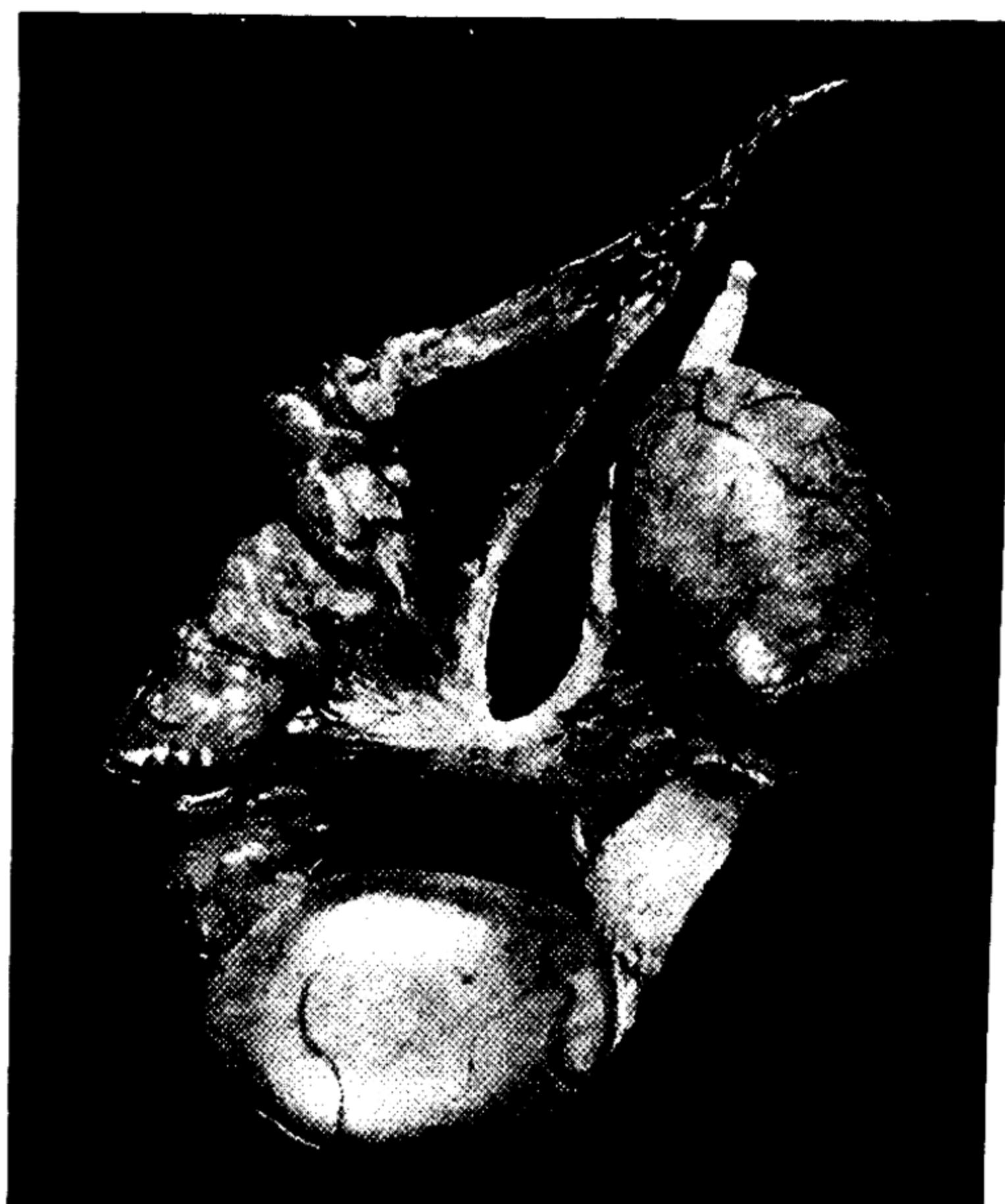


Figure 15.10. The oviduct of a hen showing the approximate configuration of the structure in the body. The oviduct carries two eggs; the upper egg lies in the uterus, and is hard shelled; the lower egg is well into the isthmus, where it is acquiring its shell membranes.

complete reproductive function of the ovary (FRAPS, HERTZ and SEBRELL, 1943). Again, BRANT and NALBANDOV (1952) have reported that full albumen secretory activity of the magnum may require, in addition to oestrogen, progesterone or a progestin.

The oviduct of the laying hen is a highly differentiated organ, as might be expected from the fact that the ovulated yolk, in passing through the oviduct, acquires all the remaining structures of the completed egg. Five regions are usually recognized (Warren and Scott, 1935a; RICHARDSON, 1935). These regions may be recognized in *Figure 15.11*.

EGG PRODUCTION AND FERTILITY IN POULTRY

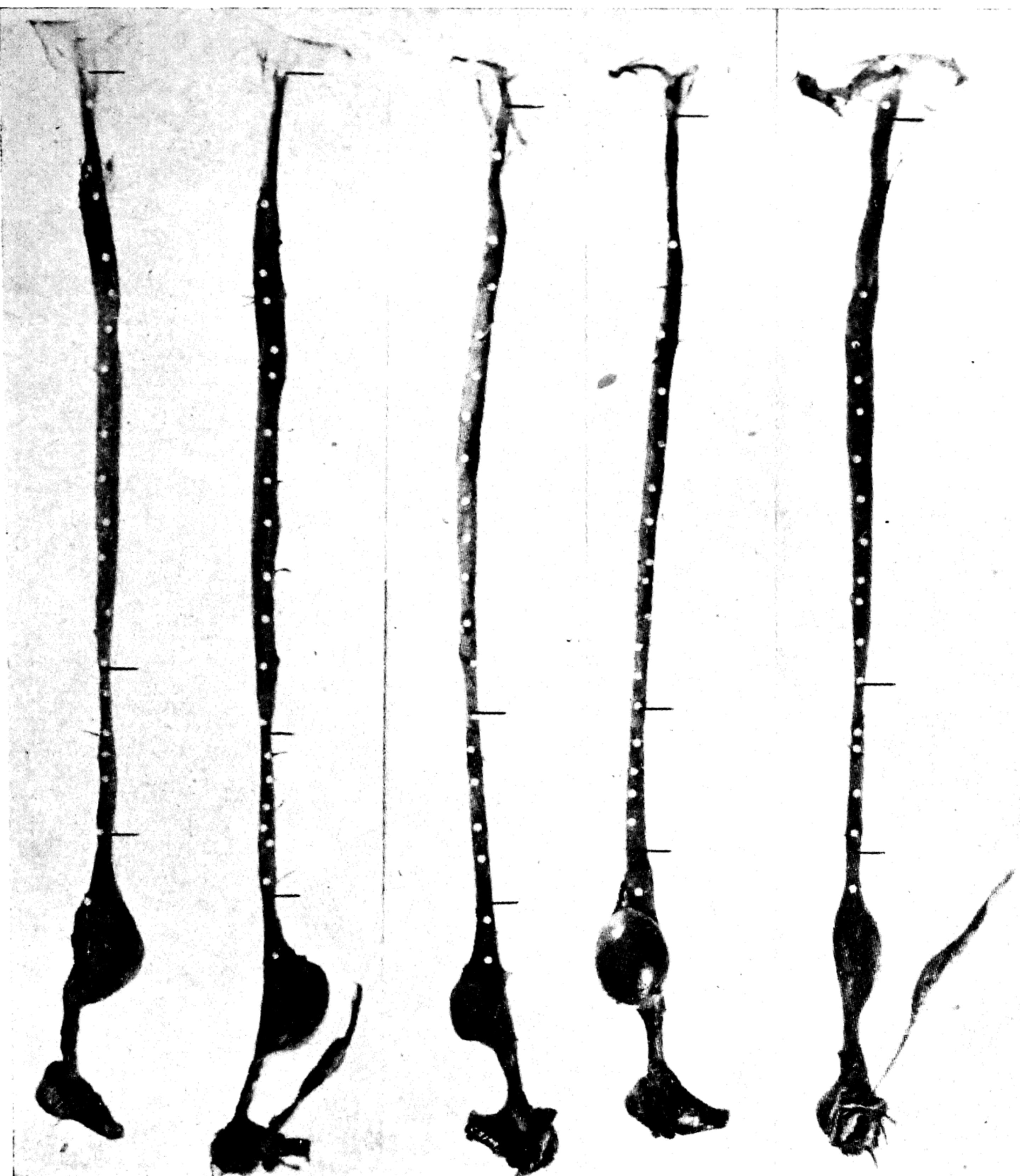


Figure 15.11. Oviducts from five hens in which records were secured on rate of passage of eggs through the organ. The white dots mark the positions of the eggs at fifteen-minute intervals. The horizontal black lines mark the limits of the infundibulum, magnum, and isthmus. Two of the birds used chanced to possess small right oviducts. (From Warren and Scott (1935), by courtesy *Poult. Sci.*)

The infundibulum

This is known also as the funnel, or mouth of the oviduct, a region of only a few centimetres in length. The funnel engulfs the ovulated yolk very soon after it is freed from the ovary; the process begins, according to Warren and Scott (1935a) within about 3 minutes, and requires about 13 minutes for completion. The enclosed ovum requires an additional 18 minutes to clear the infundibulum. Fertilization of the ovum takes place in the infundibulum (Olsen and Neher, 1948). The timing of fertilization relative to the preceding course of maturation of the ovum may be seen in *Figure 15.9*.

The infundibulum is intensely active some time before and at the time of ovulation; Warren and Scott (1935a) state that the most pronounced evidence of impending ovulation is the high state of activity of the cephalic end of the oviduct. Activity of the funnel is certainly associated with ovulatory processes, but whether the stimulus comes from the anterior pituitary body or from a hormone secreted by the follicle in process of ovulating seems not to have been established.

The magnum

The magnum, or albumen secreting region of the oviduct, is by far its longest (*Figure 15.11*) measuring some 30–50 cm. or so in length. Anteriorly, it is not easy to recognize the line of demarcation between the infundibulum and the magnum; Warren and Scott (1935a) include all of the 'mucous bearing' section, characterized by folds, in the magnum. Posteriorly, the magnum is clearly set off from the following region, the isthmus, by a narrow, translucent band when the oviduct is distended by an egg. The egg requires less than three hours to traverse the magnum (Warren and Scott, 1935a).

As might be expected in view of its albumen secreting function, the magnum is a highly glandular region (Romanoff and Romanoff, 1949). The secretory activity of the magnum is reviewed by Sturkie (1954), and by WARREN (1949). The possible dependence of secretory activity (avidin and albumen) in the magnum upon a second steroid, in addition to oestrogen, has been noted. It is of interest in this connection that avidin is secreted only by the magnum (FRAPS, HERTZ and SEBRELL, 1943).

The isthmus

This is a relatively short region of the oviduct (approx. 10 cm.), somewhat narrower than the albumen secreting magnum, and is characterized by lower longitudinal folds. The easily recognized cephalic boundary of the isthmus was described in connection with the magnum; the line of caudal demarcation is just above the outpocketing of the uterine region (*Figure 15.11*). Internally, the posterior boundary

of the isthmus is seen as the terminal limit of its longitudinal folds. Both the inner and outer membranes of the egg are formed in the isthmus in the 74 minutes required by the egg to pass through the region. It was at one time thought that some albumen was added to the egg during its passage of the isthmus, but this view has not been confirmed. A very small amount of water may be taken up during transit of the isthmus by either the hen's or the turkey's egg (BURMESTER, 1940; ASMUNDSON, 1939).

The uterus

The heavy, muscular uterus, is only some 10 or 12 cm. in length; its posterior boundary appears in the beginning of a constricted region forming the vagina. The time required by the egg to traverse the regions of the oviduct anterior to the uterus is no more than 4 or 5 hours; in contrast, the egg remains in the uterus some 18 to 20 hours or longer (Warren and Scott, 1935a), *i.e.* it spends some 80 per cent of the time of egg formation in the uterus. The weight of the albumen is approximately doubled, by the uptake of uterine fluid (salts and water), within the first 8 hours of the egg's sojourn in the uterus (Burmester, 1940). When the egg enters the uterus, its membranes surround it loosely, at completion of the period of uptake of uterine fluids, the egg is 'plumped' and the membranes tightly smoothed. The rate of calcium deposition is initially low, but increases gradually during the first several hours of the egg's stay in the uterus; from about the fifth or sixth hour, calcium deposition (or shell formation) proceeds at a fairly constant rate until the egg is laid (Burmester, 1940; BRADFIELD, 1951).

No protein appears to be added to the egg by the uptake of uterine fluid (SCOTT, HUGHES and WARREN, 1937; see also Warren, 1949). Much of the differentiation of albumen laid down in the magnum into the characteristic layers and structures found in the laid egg does occur, however, while the egg is in the uterus. This subject has been reviewed by Romanoff and Romanoff (1949), Warren (1949) and Sturkie (1954); the admirable paper by Burmester (1940) may also be consulted. An interesting account of formation of the chalazae is given by CONRAD and PHILLIPS (1938).

The uterus is also largely responsible for lay or oviposition of the completed egg; this is accomplished by contraction of the muscular walls, which forces the egg through the vagina. The abdominal musculature may also participate in oviposition (SYKES, 1954). The appropriate timing of normal oviposition is obviously important. As was noted earlier, both the ruptured and the ovulating follicle appear to be involved in the timing of oviposition; these and other factors are discussed later.

The vagina

The terminal region of the oviduct, the vagina, is 10 to 12 cm. in length, and of relatively small diameter; it forms a passage from the uterus to the cloaca. At oviposition, the vagina is everted, and the egg does not pass through the cloaca. The vagina is also everted at copulation, receiving the sperm ejaculate directly. In artificial insemination, the vagina is caused to be everted by manual means, and thus receives the sperm much as in the course of natural mating (BURROWS and QUINN, 1939).

CYCLICAL RELATIONSHIPS IN OVIPOSITION AND OVULATION

In the regularly laying hen, cyclical behaviour is exhibited at each of a number of 'levels', such as oviposition, ovulation, OIH release and yet others. We may therefore speak of the oviposition cycle, the ovulation cycle, and so on, recognizing that each of these cycles is only a specific aspect of what might be termed *the* cycle in egg production (cf. Nalbandov, 1953a). Definite relationships exist, however, between corresponding events in cycles of different orders. An understanding of these relationships, as cyclical rather than as isolated correspondences, will go far toward clarification of some of the more obscure aspects of the processes of egg production in at least the domestic fowl. Although this analysis is limited to the fowl, the general relationships dealt with probably apply equally to the turkey, since Kosin and Abplanalp (1951) have shown that 'the pattern of egg laying' in this species is essentially similar to that of the hen.

The most accessible of all the 'cycles' is of course the oviposition cycle. Of itself, the oviposition cycle is of little interest. However, the time relationships appearing in oviposition cycles afford a basis for at least a generalized formulation of timing in the ovulation cycles; these in turn form the basis for examination of relationships and events which determine ovulation. The characteristics of the cycle, as the concept is employed here, will therefore be described in some detail as they are expressed in oviposition.

THE OVIPOSITION CYCLE AND SEQUENCES

Under usual conditions of lighting and maintenance, hens even in regular production may vary greatly in their laying behaviour. Nevertheless, many hens lay their eggs in fairly characteristic patterns. Some oviposition records, most of which were selected for regularity, are reproduced in Table 15.1. The records are for battery caged hens maintained under lights from 6 a.m. to 8 p.m. The birds were observed at hourly intervals from 7 a.m. to 4 p.m. Mean time of

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oviposition was therefore 0.5 hour earlier than hour of recorded lay between 8 a.m. and 4 p.m. The first recording of the day, 7 a.m., included eggs laid between 4 p.m. of the previous day and 7 a.m. of the day of record. The time of lay of such eggs is therefore not known, but is known (within an hour) for all eggs laid between 7 a.m. and 4 p.m. of each day. Something over 90 per cent of all eggs are laid within these hours at Beltsville.

As understood here, the oviposition cycle* consists of the number of days on which oviposition occurs (1 or more) plus the number of days on which oviposition fails to occur (also 1 or more) before the resumption of oviposition. The number of ovipositions in the cycle, or the number of days on which oviposition occurs singly or consecutively, is denoted n ; the number of days intervening before the resumption of oviposition is denoted z . Length of cycle (in days) is therefore $n + z$. The frequency of oviposition within any cycle is given by

$$f = n/(n + z),$$

which corresponds to the expression for ovulation frequency earlier described by ROTHCILD and FRAPS (1945).

TABLE 15.1
SOME SELECTED EGG LAYING RECORDS IN THE HEN

The recorded hour of lay signifies that the egg was laid during the preceding hour.

Light faced figures indicate morning hours (12 noon included), bold faced figures refer to afternoon hours. The day or days of missed lay are designated by a dash.

Example	<i>Day of Record</i>															
	<i>Hour of Record</i>															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	4	—	—	2	—	—	2	—	—	4	—	—	12	—	—	1
2	1	—	12	—	1	—	12	—	1	—	1	—	2	—	1	—
3	10	2	—	10	3	—	10	2	—	10	2	—	10	3	—	9
4	9	11	3	—	9	12	4	—	9	11	3	—	10	1	4	—
5	9	10	1	4	—	8	10	11	3	—	9	10	12	3	—	8
6	8	10	12	1	4	—	9	10	11	12	4	—	8	10	11	12
7	8	9	10	10	11	11	11	12	12	12	11	11	11	1	4	—
8	10	4	—	—	—	12	—	—	—	—	—	8	11	4	—	—

Reference to the oviposition records of Table 15.1 will serve to illustrate this notion of the cycle. In example 1, the cycle includes only a single oviposition (or a single day on which oviposition occurs) plus 2 days on which oviposition fails to occur before another

* For a discussion of other concepts of the cycle, clutch and rhythm in egg production, see Romanoff and Romanoff (1949).

oviposition appears. Here $n = 1$, $z = 2$ and cycle length, $n + z = 1 + 2$ or 3 days. Cycle frequency, f , is equal to $n/(n + z) = \frac{1}{3} = 0.33$. In example 2, the cycle again includes only a single oviposition, but here only a single day on which the event fails to take place before oviposition recurs. In this case $n = 1$, $z = 1$, cycle length = 2 (days), and $f = n/(n + z) = \frac{1}{2}$ or 0.50. In example 3, oviposition occurs on each of two consecutive days ($n = 2$), and only a single day elapses before the resumption of oviposition ($z = 1$). Cycle length is thus 3 (days), and $f = \frac{2}{3}$ or 0.67. In examples 4 to 6 of the Table, n increases, but $z = 1$ in all cases.

The Closed Cycle

The cycle in which $z = 1$, regardless of the value of n ($n > 1$) is of especial interest here because of the definitive order of follicular maturation which can be recognized in such cycles. The cycle in which $z = 1$ may be described as a *closed* cycle. Unless specifically noted to the contrary, the term cycle throughout the remainder of this paper will imply the closed cycle. Since $z = 1$ in the closed cycle, cycle length is always equal to $n + 1$, and

$$f = n/(n + 1)$$

The least possible value of $n/(n + 1)$ is $\frac{1}{2}$ or 0.50, as appears in example 2 of Table 15.1. It is of interest that the value of the expression $n/(n + 1)$ approaches unity as a limit. In the closed cycle then, the frequency of oviposition can vary only between 0.50 and 1, regardless of the value of n .

The Sequence

The oviposition cycle, as has been observed, may include only a single oviposition ($n = 1$). But more commonly, the cycle in regularly laying hens includes two or more ovipositions, these occurring on a number (n) of consecutive days to constitute a sequence. Sequences of 2 to 16 members are shown in examples 3 to 7, Table 15.1. A sequence of ovipositions may stand in relative isolation (separated, that is, from other such sequences or ovipositions by a number of days on which oviposition does not occur); such a sequence is included in the last record (days 12-14) of Table 15.1. Our immediate concern is with the characteristics of the sequence as these appear in the closed cycle.

The first oviposition of any sequence (or cycle) is designated the C_1 , the second the C_2 , and so on. The last or terminal member of a sequence is referred to as the C_n (sometimes, also as the C_t); it is convenient also to recognize the next to last oviposition as the C_{n-1} (or C_{t-1}). The same designations apply to the egg, ovulation, the ovulating follicle, and other aspects of cyclical (or sequential) behaviour.

Lag

Except in lengthy sequences, each oviposition beyond the first (or C_1) takes place later in the day than did its predecessor (ATWOOD, 1929a, b; HAYS, 1936; HEYWANG, 1938; BERG, 1945). The records of Table 15.1 illustrate this fact. This difference in *times of day* at which ovipositions occur on consecutive days has been denoted 'lag', as was the corresponding retardation in the ovulation cycle (FRAPS, 1954a, b, c). In mid-regions of lengthy sequences, lag may approach or equal zero or even become negative (example 7 of Table 15.1), although ovipositions near the beginning and towards the end of such sequences exhibit the more extensive lag typical, in varying degrees, of shorter sequences.

It is important to note that lag is not the interval between successive ovipositions, but the clockwise difference in times of day of one oviposition with respect to its predecessor. The interval between successive ovipositions is therefore $24 + h$, where h is expressed in hours (cf. Atwood, 1929). Lag is implicit in the 'asynchronous rhythm' of BASTIAN and ZARROW (1952), for this rhythm is asynchronous, from day to day, by the extent of lag.

Since lag is defined as the difference in times of day between consecutive ovipositions (or other events), it is obvious that we may speak also of cumulative lag, total lag, or mean lag in the sequence or cycle.

Cumulative lag is the sum of individual lag values taken to each successive place in a sequence, which is the same as differences in times of day between the first and each subsequent oviposition taken in order. Thus in the first sequence of example 5, Table 15.1, cumulative lag, in hours, follows as 1, 2, 3, 4, 7.

Total lag is the sum of all individual lag values in the sequence; it is therefore the same as the last term in the series of cumulative lag values (7 hours in the above series). Total lag is even more simply read as the difference in times of occurrence of first and last ovipositions in a sequence. Using the above noted example, total lag is equal to the difference between 9 a.m. and 4 p.m., or 7 hours.

Mean lag in a sequence is total lag (in hours) divided by the number of places ($n-1$) at which lag can occur. In the first sequence of example 5, total lag is 7 hours, length of sequence (n) is 4, and lag occurs at $n-1$, or 3 places. Mean lag is thus equal to $\frac{7}{3}$ or 2.33 hours.

In the cycle in which $n = 2$, lag can occur at only one place, the second of the sequence (example 3 of Table 15.1). Cumulative, total and mean lag in such sequences are therefore identical.

As was noted earlier, the interval between successive ovipositions in the sequence is $24 + h$ hours, where h represents lag. The mean

interval in the sequence is thus 24 hours + mean lag in hours. It is of some interest that Atwood (1929a) recorded his data in this form.

Calculation of Intervals and Lag in Oviposition Sequences

The relationships between times of oviposition, intervals and lag can perhaps be seen more concretely if we carry through several simple operations in representative sequences. For this purpose we have used the laying records of a group of White Leghorn hens, all in second or third years of production, during the period February 22–March 31 (1949). The birds were individually caged in laying batteries, with feed and water available *ad lib.* Lights were maintained from 6 a.m. to 8 p.m., and eggs laid were recorded at 0.5 hourly intervals throughout the same hours. Times of oviposition were assumed to be 0.25 hour earlier than recorded times of lay, except in the case of 6 a.m. eggs, for which times of oviposition were unknown. Mean times of oviposition of eggs in all complete sequences of 2 to 6 members were computed from these records, and are recorded in Table 15.2. The number of completed sequences on which the figures are based is given in the last column of the Table; this number obviously declines rapidly as n increases from 2 to 6.

TABLE 15.2
TIMES OF DAY OF SUCCESSIVE OVIPOSITIONS IN SEQUENCES OF WHITE LEGHORN HENS
(Beltsville)

<i>n</i>	<i>Ovipositions</i>						<i>Number of Sequences</i>
	<i>C₁</i>	<i>C₂</i>	<i>C₃</i>	<i>C₄</i>	<i>C₅</i>	<i>C₆</i>	
2	10.25	2.57	—	—	—	—	694
3	9.19	12.02	4.00	—	—	—	399
4	8.46	10.45	12.41	4.09	—	—	105
5	8.28	10.06	11.34	1.05	4.13	—	28
6	8.31	10.29	11.36	12.23	1.48	4.40	12

Light faced figures, morning hours; bold faced figures, afternoon hours.

Table 15.3 gives the intervals between successive ovipositions recorded in Table 15.2, together with mean intervals, for sequences of differing lengths. Our data are similar, in all important respects, to those of Atwood (1929), Hays (1936), Heywang (1938) and Berg (1945). The decrease in length of intervals with increasing sequence length (n) is evident both in individual intervals at corresponding places in the sequences and in mean length of intervals for the sequences. The relatively greater interval between the last two ovipositions in all sequences of three or more members is notable, and has often been remarked upon.

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Lag at successive places, total lag and mean lag are recorded in Table 15.4 for the same sequences appearing in Tables 15.2 and 15.3.

TABLE 15.3

INTERVALS BETWEEN SUCCESSIVE OVIPOSITIONS IN THE SEQUENCES OF
WHITE LEGHORN HENS (Beltsville)

n	Intervals (in hours)					Mean Interval
	C_1 to C_2	C_2 to C_3	C_3 to C_4	C_4 to C_5	C_5 to C_6	
2	28.53	—	—	—	—	28.53
3	26.72	27.97	—	—	—	27.34
4	25.98	25.93	27.47	—	—	26.46
5	25.63	25.47	25.52	27.13	—	25.94
6	25.97	25.12	24.78	25.54	26.87	25.63

Individual lag values are calculated from Table 15.2 as *differences in times of day* between successive ovipositions, total lag as difference in times of day between first and last ovipositions in each sequence. Mean lag is then found as total lag divided by the number of places of lag, which, as was noted earlier, is $n-1$ in any sequence.

TABLE 15.4

LAG (IN HOURS) IN OVIPOSITION SEQUENCES OF WHITE LEGHORN HENS (Beltsville)

n	Lag at successive places					Total lag	Mean lag
	h_2	h_3	h_4	h_5	h_6		
2	4.53	—	—	—	—	4.53	4.53
3	2.72	3.97	—	—	—	6.68	3.34
4	1.98	1.93	3.47	—	—	7.38	2.46
5	1.63	1.47	1.52	3.13	—	7.75	1.94
6	1.97	1.12	0.78	1.42	2.87	8.42	1.63

Individual lag values may be calculated alternatively from the data of Table 15.3 by simply subtracting 24 hours from recorded intervals. Similarly, mean lag for each sequence is the difference between the mean interval (Table 15.3) and 24 hours. Total lag is then found as mean lag times the number of places of lag ($n-1$) in each sequence.

Heywang (1938), following Atwood (1929a, b), published extensive observations on the interval between lay of successive eggs by pullets and hens over a 13-month period, under conditions of natural daylight at Glendale, Arizona. His Table 3 gives, for White Leghorns, the mean time intervals between oviposition of successive eggs in sequences of 2 to 13 ovipositions. Corresponding lag values are obtained by subtracting 24 (hours) from the lengths of interval (in hours) given

by Heywang, as was described in connection with Table 15.4. These data, together with cumulative and total lag, are shown graphically in *Figure 15.12*. Length of sequence is indicated by the numerals below each set of adjacent bars or columns; there is a single column for $n = 2$. Successive adjacent bars stand in consecutive lag places for each sequence; the number of lag places in each sequence is of course 1 less than sequence length (n). The solid portion of each

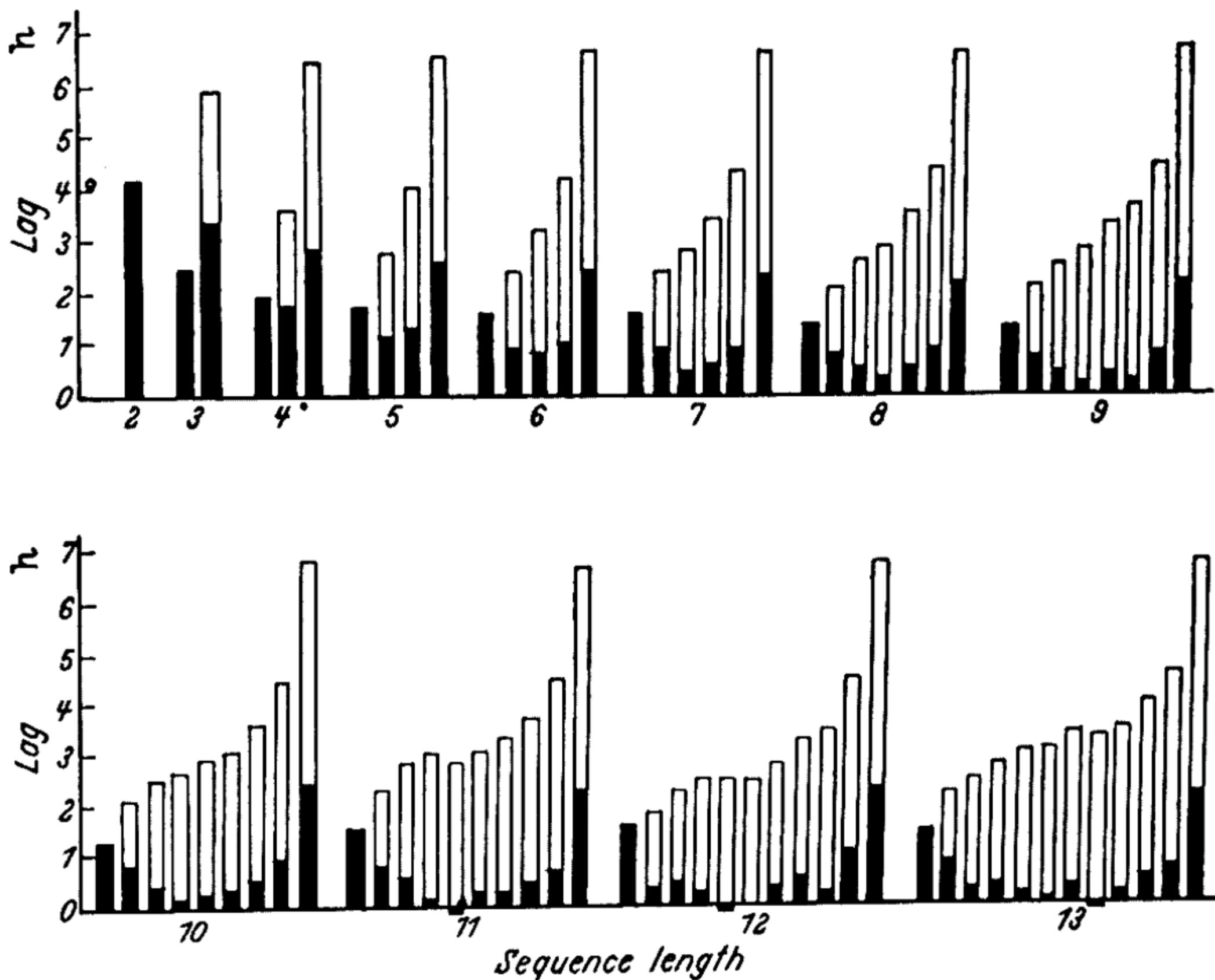


Figure 15.12. Lag in oviposition sequences, 2 to 13 members. Based on data from Heywang (1938).

bar represents individual lag; the solid plus superimposed white segments measures cumulative lag at successive lag positions. The total height of the last bar in each set of adjacent bars is of course total lag for the sequence.

The histograms of *Figure 15.12* bring out very clearly some of the characteristics of lag in, and particularly between, oviposition sequences. As was noted earlier, in all sequences of 3 or more members, lag of the terminal oviposition (or egg) is greater than at preceding places in the sequence. Lag at the terminal place is also seen to decrease as n increases from 2 to 7 or 8; thereafter it remains fairly uniform, as does total lag. As a matter of fact, the 'lag pattern' at the first 3 places, and at the last 3 places, changes but little as sequence length increases from 7 to 13. Lag between these several initial and terminating places continues to decrease, approaching or even falling slightly below zero. It is clear, from these relationships, that oviposition may continue indefinitely without increase in total lag for the sequence.

Diurnal Periodicity

The fact that eggs are usually laid during daylight hours is common knowledge (WARREN and Scott, 1936). Total lag in the sequences of Table 15.4 and in the histograms of *Figure 15.12*, tells us that oviposition occurred, on the average, within fairly restricted hours of the 24, and also that it did not occur within the remaining hours. The significance of diurnal periodicity, thus expressed in the oviposition sequence, can be better appreciated as it appears in the ovulation and OIH release cycles.

TIMING IN THE OVULATION SEQUENCES

There is no known method of determining exactly the time of ovulation in the hen except by observation of the exposed ovary. This was done by Warren and Scott (1934, 1935a) and Phillips and Warren (1937). The important findings recorded by these workers, together with results based on less direct procedures, have made possible a fairly satisfactory formulation of time relationships in the ovulation sequence (and cycle) from timing in the oviposition sequences.

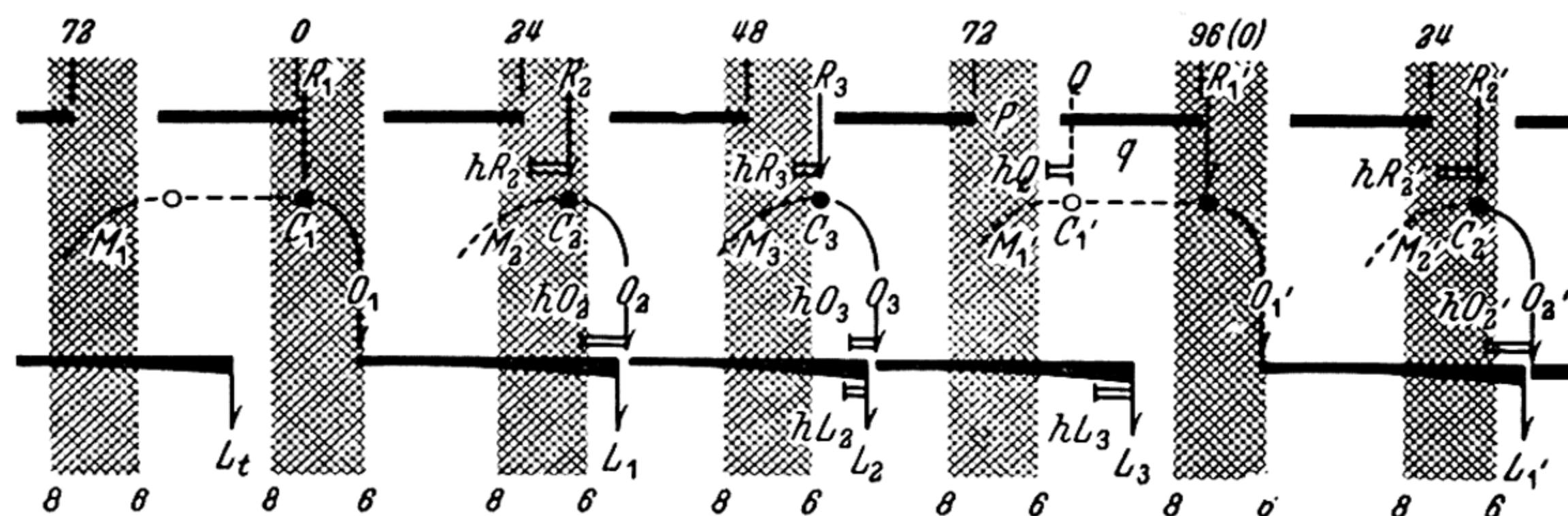


Figure 15.13. Time relationships between OIH release, follicular maturation, ovulation and oviposition in a 4-day cycle ($n = 3$).

The order of events with which we have to deal is represented schematically in the lower part of *Figure 15.13*. Here O_1 , O_2 and O_3 represent a sequence of ovulations which, following a single day of 'missed' ovulation, is repeated by O_1' , O_2' (and O_3' , not shown in the *Figure*). The passage of each egg through the oviduct is indicated by the heavy, horizontally disposed devices which are terminated by ovipositions L_1 , L_2 , L_3 and L_1' . It is clear that relatively short intervals separate the lay of one egg and ovulation of the succeeding follicle within the sequence (L_1 to O_2 and L_2 to O_3 in the *Figure*); a much greater interval (L_3 to O_1') occurs between the terminal oviposition of a sequence and the C_1 ovulation (O_1') of the next sequence. The short interval between lay of an egg and the succeeding ovulation is designated the interval between lay and associated ovulation; its value determines the time relationships between oviposition and ovulation at all places except the first of the ovulation sequence.

The Interval, Lay to Associated Ovulation

Warren and Scott (1935a) and Phillips and Warren (1937) observed White Leghorn hens for time of oviposition, celiotomized the birds as soon as possible following lay, and noted the time of associated ovulation. The mean interval from lay to associated ovulation was found by Warren and Scott to be 30.7 minutes (range 14 to 75 minutes), by Phillips and Warren, 32.2 minutes (range 7 to 74 minutes). The interval was determined in 56 hens in the two groups of observations; 51.8 per cent of all ovulations occurred within 30 minutes of preceding lay. McNALLY and BYERLY (1936) sacrificed 32 White Leghorn hens 30 minutes following lay and found ovulation to have occurred within this interval in 20 or 62.5 per cent, a result in good accord with the earlier findings of Warren and Scott.

Phillips and Warren noted that the interval between lay and associated ovulation was correlated with mean length of interval (within sequences) between successive eggs. Their data, in terms of mean lag (rather than mean intervals) are shown in *Figure 15.14*.

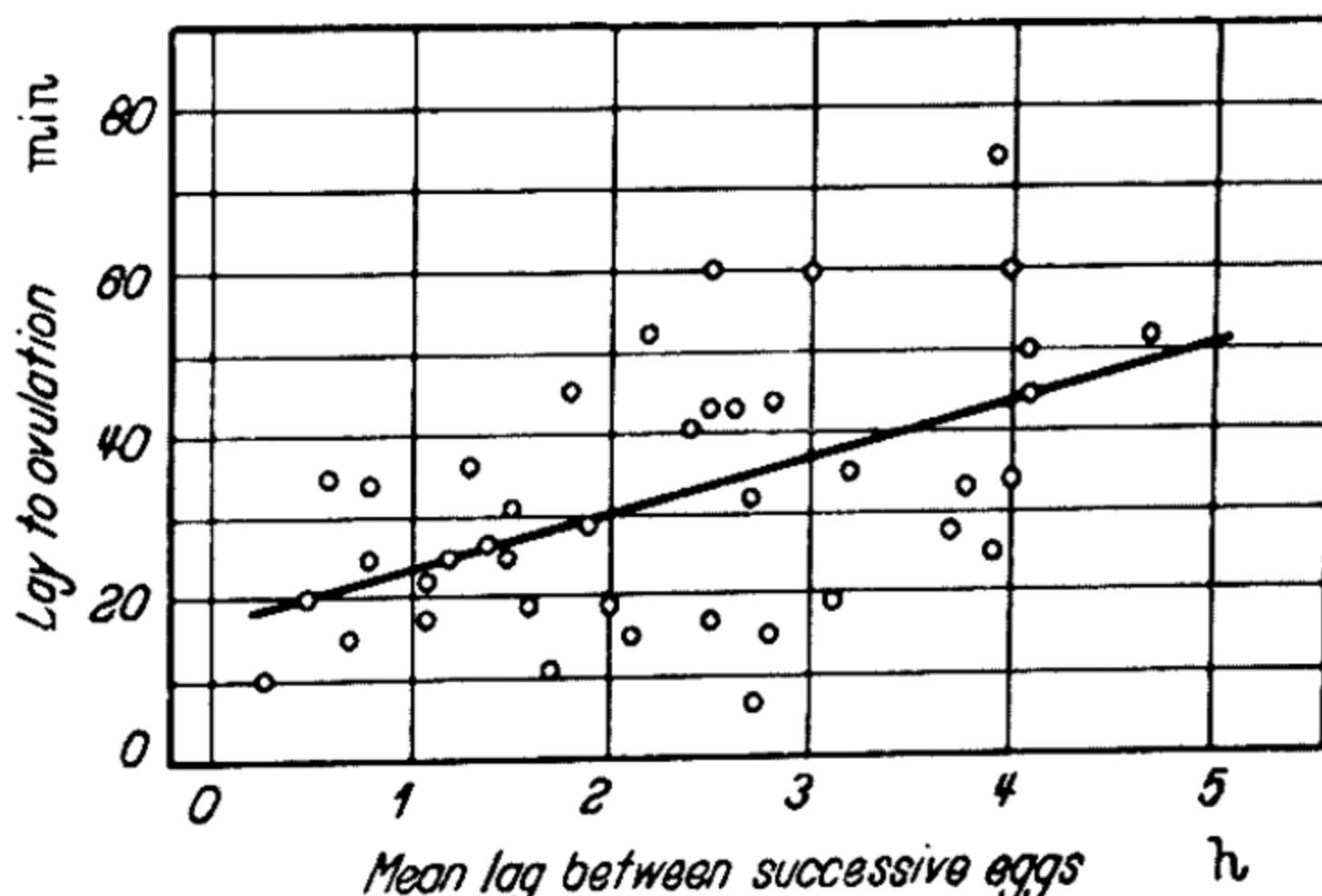


Figure 15.14. Relation of the interval, lay to associated ovulation, to estimated mean lag between successive ovipositions. Based on data from Phillips and Warren (1937).

Using Heywang's data for mean lag at different sequence lengths, the variation of the interval between lay and associated ovulation with length of sequence (n) has been estimated from the equation for the regression curve shown in *Figure 15.14*, and is recorded in Table 15.5 for $n = 2$ to 6. The mean intervals from lay to associated ovulation are seen to decrease with increasing sequence length. The indicated values for intervals, lay to associated ovulation at given sequence lengths, are probably not too accurate (even as mean values), but they serve to give some weight to the longer intervals in the shorter sequences. Neher, Olsen and Fraps (1950) recorded a somewhat longer interval than is given in Table 15.5 for the 2-egg sequence, but their data were not based on direct observation of time of

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associated ovulation. In the following discussion it will be convenient to accept the intervals given in Table 15.5, and to suppose also that the interval from lay to associated ovulation is the same at all places in sequences of given length.

TABLE 15.5
SEQUENCE LENGTH (n), OVULATION FREQUENCY (f), MEAN LAG AND THE MEAN
INTERVAL BETWEEN LAY AND ASSOCIATED OVULATION

n	f	Mean lag Hours	Lay to associated ovulation (i)	
			Hours	Minutes
2	0.67	4.21	0.75	45.0
3	0.75	2.97	0.61	36.7
4	0.80	2.16	0.52	31.4
5	0.83	1.67	0.47	28.1
6	0.86	1.35	0.43	26.0

Time Relations Between C_s Ovulations and Oviposition

It is clear that time of any C_s ovulation (C_2 , C_3 , etc.) is later than time of the preceding oviposition (C_1 , C_2 , etc., but excluding the C_n) by the value assigned to the interval, lay to associated ovulation. This interval, incidentally, is often taken as 0.5 hour, or sometimes as an hour or less, rather than 'adjusted' to sequence length as in Table 15.5.

Intervals between successive ovulations can of course be calculated directly from times of ovulation where these are known. If, however, we assume the interval from lay to associated ovulation to be constant, the interval between any pair of successive ovulations (except that between the C_1 and the C_2) is the same as is the interval between the preceding pair of ovipositions. This can be seen by reference to *Figure 15.13*. Here the interval between O_2 and O_3 consists of the time elapsing between O_2 and L_2 plus the succeeding interval between lay and associated ovulation (L_2 to O_3). Similarly, the interval between L_1 and L_2 includes the time elapsing between O_2 and L_2 plus the preceding interval between lay and associated ovulation (L_1 to O_2). Since the intervals L_1 to O_2 and L_2 to O_3 are assumed to be constant, and O_2 to L_2 is a common term, the interval between the pair of ovulations, O_2 and O_3 , is equal to the interval between the preceding pair of ovipositions, L_1 and L_2 . The same relationship holds for all subsequent pairs of ovulations in longer sequences. There is of course no interval between successive ovulations corresponding to the interval between the last pair of ovipositions (L_{n-1} to L_n), since the last oviposition is not followed by associated ovulation.

As was pointed out in describing the oviposition sequences, lag is found by subtracting 24 hours from the interval between any pair of successive ovipositions. Referring again to *Figure 15.13*, the interval O_2 to O_3 is seen to consist of 24 hours plus lag, hO_3 , and the interval L_1 to L_2 of 24 hours plus lag, hL_2 . Since the intervals O_2 to O_3 and L_1 to L_2 are equal, lag at the C_3 ovulation (hO_3) must equal lag at the C_2 oviposition (hL_2). The more general statement is that lag at any place in the ovulation sequence (except the C_2) is equal to lag at the preceding oviposition.

The Timing of C_1 Ovulation

Warren and Scott (1935b) first demonstrated that the C_1 ovulation of a sequence occurred during early morning hours, presumably at an earlier hour than did any subsequent ovulation. FRAPS and DURY (1943a) reported that C_1 ovulation occurred between 4 and 7 a.m. These hours were 'Eastern War Time' (E.W.T.), but since

TABLE 15.6

ESTIMATION OF TIME OF OVULATION FROM PLACE OF OVUM IN THE MAGNUM OF AUTOPSIED HENS*

<i>Regional level</i>	<i>Time from ovulation Minutes</i>	<i>Inter-level differences Minutes</i>
0	30	10
0.1	40	12
0.2	52	14
0.3	66	18
0.4	84	21
0.5	105	21
0.6	126	21
0.7	147	21
0.8	168	21
0.9	189	21
1.0	210	—

* In estimating time of ovulation, the oviduct is laid out as shown in *Figure 15.11*, the total length of magnum (m) is measured, and the distance from beginning of the magnum to the *anterior* end of the contained egg (e) is determined. 'Place of egg' is the ratio e/m , which is usually carried to two decimal places. The 'regional level' given by the first figure in this ratio and the corresponding time from ovulation are found in the table; to this time is added the proportional part of inter-level differences represented by the second decimal of the observed ratio for place of egg.

the lighting schedule was likewise maintained on E.W.T., these figures hold for the standard conditions noted earlier (lights 6 a.m. to 8 p.m.). In other papers from this laboratory, C_1 ovulation has been stated to occur at various hours, but usually within the range indicated by Fraps and Dury. Differences in indicated hours arise

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largely out of differences in the laying behaviour of hens selected for various experimental objectives.

Our first estimates of time of C_1 ovulation were based on sacrifice and autopsy of selected hens at stated hours. Later, the time of C_1 ovulation was estimated from place of the egg in the oviduct of sacrificed hens. This latter procedure was suggested by observations of Warren and Scott (1935a) indicating that the egg traversed the magnum of the oviduct in a fairly characteristic fashion (see *Figure 15.11*). Using the data of Table 15.5 to establish time of C_1 ovulation, the place of C_1 eggs in the magnum at known times thereafter was ascertained by sacrificing the hen, removing the oviduct, and determining the relative place in the magnum at which the egg was found. From these findings (based upon several hundred sacrificed hens), a curve was constructed indicating place of egg at known times following the preceding ovulation; from this curve, Table 15.6 (unpublished) was formulated to estimate time of any ovulation from place of the egg in the magnum. The usual procedure in estimating time of C_1 ovulation was to palpate the hen at hourly intervals until the egg was known to be in the magnum, sacrifice the bird, determine 'place in magnum', and calculate time of C_1 ovulation from Table 15.6.

TABLE 15.7

TIME OF C_1 OVULATION IN WHITE LEGHORN HENS UNDER CONTROLLED LIGHTING
AND UNDER SAME LIGHTING PLUS NATURAL DAYLIGHT (August)

n	Number of hens	3	% of hens ovulating at indicated hour (a.m.)*						Later
			4	5	6	7	8		
<i>Lights 6 a.m. to 8 p.m. (February-March)</i>									
2	31	—	26	39	19	3	6	6	
3	23	—	22	57	13	9	—	—	
<i>Lights 6 a.m. to 8 p.m. plus daylight (August)</i>									
2	48	4	23	23	42	2	4	2	
3	15	—	—	40	33	20	7	0	
>3	15	—	13	20	60	7	0	0	

* The percentage of hens ovulating 0.5 hour before and 0.5 after the indicated hour.
'Later' includes ovulations occurring after 8.30 a.m.

The time of C_1 ovulation, as estimated from place of egg in the magnum, is recorded in Table 15.7 (unpublished) for conditions indicated in the legend. There is considerable spread in the hour of C_1 ovulation, as there was in the time of C_1 oviposition in the same hens prior to sacrifice. It will be noted that C_1 ovulation occurs at an earlier hour as n increases from 2 to 3. The later hour of C_1 ovulation, in sequences of equal length, in hens autopsied during August is also to be noted. These hens were under standard electric

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lighting, but daylight was not excluded; during August, daylight extends somewhat beyond the 8 p.m. cut-off of the electric lights. The hour of C_1 ovulation apparently became later in association with the later onset of darkness, as was subsequently demonstrated in other connections.

While it was not too difficult to determine the approximate or mean time of C_1 ovulation for a given set of experimental conditions (and hens), a more general association of time of C_1 ovulation with some characteristic of the sequence (or cycle) was desirable on theoretical grounds. In comparing (for individual hens) the time of C_1 ovulation with previously recorded times of lay of C_1 eggs, it could scarcely be overlooked that the difference, in times of day, between C_1 ovulation and C_1 lay was often of the same order as was the difference (again, in times of day) between lay of the last two eggs. This apparent similarity was seen in simpler terms by supposing the difference, in time of day, between the first two ovulations of a sequence to be of the same order as was the difference (in times of day) between the last two ovipositions of the same or similar sequences. This is the same as saying that lag at the second place of an ovulation sequence (hO_2) is of the same order as is lag at the terminal place in the corresponding oviposition sequence (hL_n).

TABLE 15.8

LAG AT C_2 OVULATION CALCULATED FROM KNOWN MEAN TIME OF C_1 OVULATION (FROM AUTOPSIED HENS) COMPARED WITH LAG AT THE TERMINAL (C_n) OVIPOSITION BASED ON PREVIOUS RECORDS OF LAY. TIMES OF OVULATION AND OVIPOSITION IN HENS LAYING OUT REGULAR 1-EGG CYCLES ($n=1$) ARE INCLUDED; THERE IS OF COURSE NO LAG IN THE CASE OF THE SINGLE OVULATION (OR OVIPOSITION) OF THE 1-MEMBER CYCLE

	<i>n</i>		
	1	2	3 and 4
Mean time of C_1 ovulation, a.m.	6.46	6.21	5.44
Mean time of C_1 oviposition, a.m.	11.55	9.54	8.35
Differences in times of day hours	5.15	3.55	2.85
Lay to associated (C_2) ovulation	—	0.75	0.61
Lag at C_2 ovulation (hO_2)	—	4.30	3.46
Lag at C_n oviposition (hL_n)	—	4.21	3.07

The approximate equivalence of hO_2 and hL_n in sequences of 2, 3 and 4 members is indicated in the data of Table 15.8. It is to be remembered that estimation of time of C_1 ovulation from place of egg in the magnum also involves some degree of uncertainty. The agreement between the two sets of values is accordingly about as good as might be expected. Nevertheless, the equivalence of hO_2 and hL_n

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must be looked upon as an empirical approximation rather than as a rigorous identity. With this reservation in mind, the 'equality' or 'identity' of hO_2 and hL_n affords a most convenient means of formulating one of the most important variables in ovulation (and antecedent) sequences which is otherwise difficult to describe.

ESTIMATION OF TIME VARIABLES IN OVULATION SEQUENCES

The results of the preceding examination of relationships between oviposition and ovulation may now be applied, by way of example, to estimation of time factors in ovulation sequences corresponding to time factors in oviposition sequences of the 'Beltsville Leghorns' described earlier.

The hour of C_1 ovulation in sequences of 2 to 6 members is estimated in Table 15.9 for ovipositions recorded in Table 15.2. The intervals, lay to associated ovulation (i), are from Table 15.5. Times of C_2 ovulation, as recorded in Table 15.9, are later than C_1 ovipositions

TABLE 15.9

ESTIMATION OF TIME OF C_1 OVULATION IN TERMS OF THE ASSUMED CORRESPONDENCE
OF hO_2 WITH hLn

n	Time of C_1 oviposition (a.m.)	i^* Minutes	Time of C_2 ovulation (a.m.)	hLn (= hO_2) hr. and min.	Time of C_1 ovulation (a.m.)
2	10.25	45	11.10	4.32	6.38
3	9.19	37	9.56	3.58	5.58
4	8.46	31	9.17	3.28	5.49
5	8.28	28	8.56	3.08	5.48
6	8.31	26	8.57	2.52	6.05

* i : the interval from lay to associated ovulation.

by the values of i at indicated sequence lengths. Lag of the terminal egg (hL_n) in sequences of 2 to 6 members is from Table 15.4; lag in Table 15.9 is given in hours and minutes for arithmetical convenience. Since hO_2 is assumed to be equal to hL_n , the time of C_1 ovulation is found by subtracting hL_n from the time of C_2 ovulation. It is to be understood, of course, that C_1 ovulation occurs on the day preceding C_1 oviposition (or C_2 ovulation) as would be evident if we had used intervals (Table 15.3) rather than the much more convenient lag notation.

Times of successive ovulations in sequences of 2 to 6 members, corresponding to times of successive ovipositions (Table 15.2), are given in Table 15.10. The estimated times of C_1 ovulation are from Table 15.9. Times of subsequent ovulations (C_2 , C_3 , etc.) are later in the day than the preceding oviposition by the value of the interval, lay to associated ovulation (n), characteristic of the sequence. It is

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important to remember, in estimating time of ovulations beyond the first, that a given ovulation is later than the preceding (not the same) oviposition. This means that the terminal ovulation is later, by the value of i , than the $n-1$ oviposition (Table 15.2); there is of course no ovulation associated with C_n oviposition.

TABLE 15.10
TIMES OF SUCCESSIVE OVULATIONS IN SEQUENCES OF WHITE LEGHORN HENS
(Beltsville)

n	i † (Minutes)	Ovulations					
		C_1	C_2	C_3	C_4	C_5	C_6
2	45	6.38*	11.10	—	—	—	—
3	37	5.58	9.56	12.39*	—	—	—
4	31	5.49	9.17	11.16	1.12	—	—
5	28	5.48	8.56	10.34	12.02	1.33	—
6	26	6.05	8.57	10.55	12.02	12.49	2.14

* Light faced figures, morning hours; bold faced figures, afternoon hours.

† i : the interval from lay to associated ovulation.

The intervals between the successive ovulations in the sequences (Table 15.11) may be calculated directly from times of ovulation (Table 15.10). But they may also be formulated directly by transposing intervals in corresponding oviposition sequences (Table 15.3),

TABLE 15.11
INTERVALS BETWEEN SUCCESSIVE OVULATIONS IN THE SEQUENCES, WHITE LEGHORN HENS
(Beltsville)

n	Intervals (in hours)				
	C_1 to C_2	C_2 to C_3	C_3 to C_4	C_4 to C_5	C_5 to C_6
2	28.53	—	—	—	—
3	27.97	26.72	—	—	—
4	27.47	25.98	25.93	—	—
5	27.13	25.63	25.47	25.52	—
6	26.87	25.97	25.12	24.78	25.42

as has already been noted. The interval between C_1 and C_2 ovulations is (or is assumed to be) identical with the interval between the next to last (C_{n-1}) and the terminal (C_n) ovipositions. Each remaining interval in the ovulation sequence is equal to the preceding interval in the corresponding oviposition sequence. A comparison of the ovulation intervals recorded in Table 15.11 with the oviposition intervals given in Table 15.3 will emphasize the simplicity of these transpositions.

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Lag in the ovulation sequences (Table 15.12) may be calculated from intervals recorded in Table 15.11, just as lag in oviposition sequences (Table 15.4) was calculated from corresponding intervals in the oviposition sequences (Table 15.3); but, like intervals, lag in the ovulation sequences may be recorded by simple transposition of lag values appearing in the oviposition sequences (Table 15.4). Lag in the second place of the ovulation sequence is equal to lag at the last place in the oviposition sequence (hL_n). Lag in each subsequent place in the ovulation sequence is equal to lag at the preceding place in the oviposition sequence. Combining these, we have

$$hO_2 = hL_n, hO_3 = hL_2, \dots, hO_n = hL_{n-1}$$

a formulation which is fundamental to the estimation of lag at all antecedent levels of cyclical events (e.g., *OIH* release).

TABLE 15.12
LAG (IN HOURS) IN OVULATION SEQUENCES OF WHITE LEGHORN HENS
(Beltsville)

n	Lag at successive places					Total lag	Mean lag
	h_2	h_3	h_4	h_5	h_6		
2	4.53	—	—	—	—	4.53	4.53
3	3.97	2.72	—	—	—	6.68	3.34
4	3.47	1.98	1.93	—	—	7.38	2.46
5	3.13	1.63	1.47	1.52	—	7.75	1.94
6	2.87	1.97	1.12	0.78	1.42	8.15	1.63

Graphically, the lag relationships shown in *Figure 15.12* for oviposition sequences are transposed to represent lag in corresponding ovulation sequences by (i) transferring the last individual lag of the oviposition sequence to the first place in the ovulation sequence, and (ii) moving each remaining lag value in the oviposition sequence one place to the right. Despite the simplicity of these transformations, some characteristics of lag in the ovulation sequences (*Figure 15.15*) differ conspicuously from the expressions of lag in the oviposition sequence (*Figure 15.12*). The most notable is, of course, the relatively greater value of lag in the second place of the ovulation sequence (hO_2). In consequence largely of this greater value of hO_2 lag 'accumulates' much more rapidly in the ovulation than in the oviposition sequence. Nevertheless, there appears in the terminal place or two of all ovulation sequences of 4 or more members a small but definite increase in lag.

The lag relationships shown in *Figure 15.15* are remarkably consistent, both within and between sequences. This might be expected of lag relations involving hO_3 (the second lag column of sequences of

2 or more members) and subsequent places, for these represent the same magnitudes, and occur in the same order, as do the corresponding members of oviposition sequences. The 'consistent' place of hO_2 (the *first* lag column of each sequence) as a member of these successions is, however, a different matter. Looking particularly at sequences of 6 or more members (*Figure 15.15*), the greater value of hO_2 seems certainly to be 'expected' in view of relationships existing between the remaining members of these sequences. Estimated values of hO_2 might indeed be even greater in these (and shorter) sequences, but they could not be much less than shown without introducing some

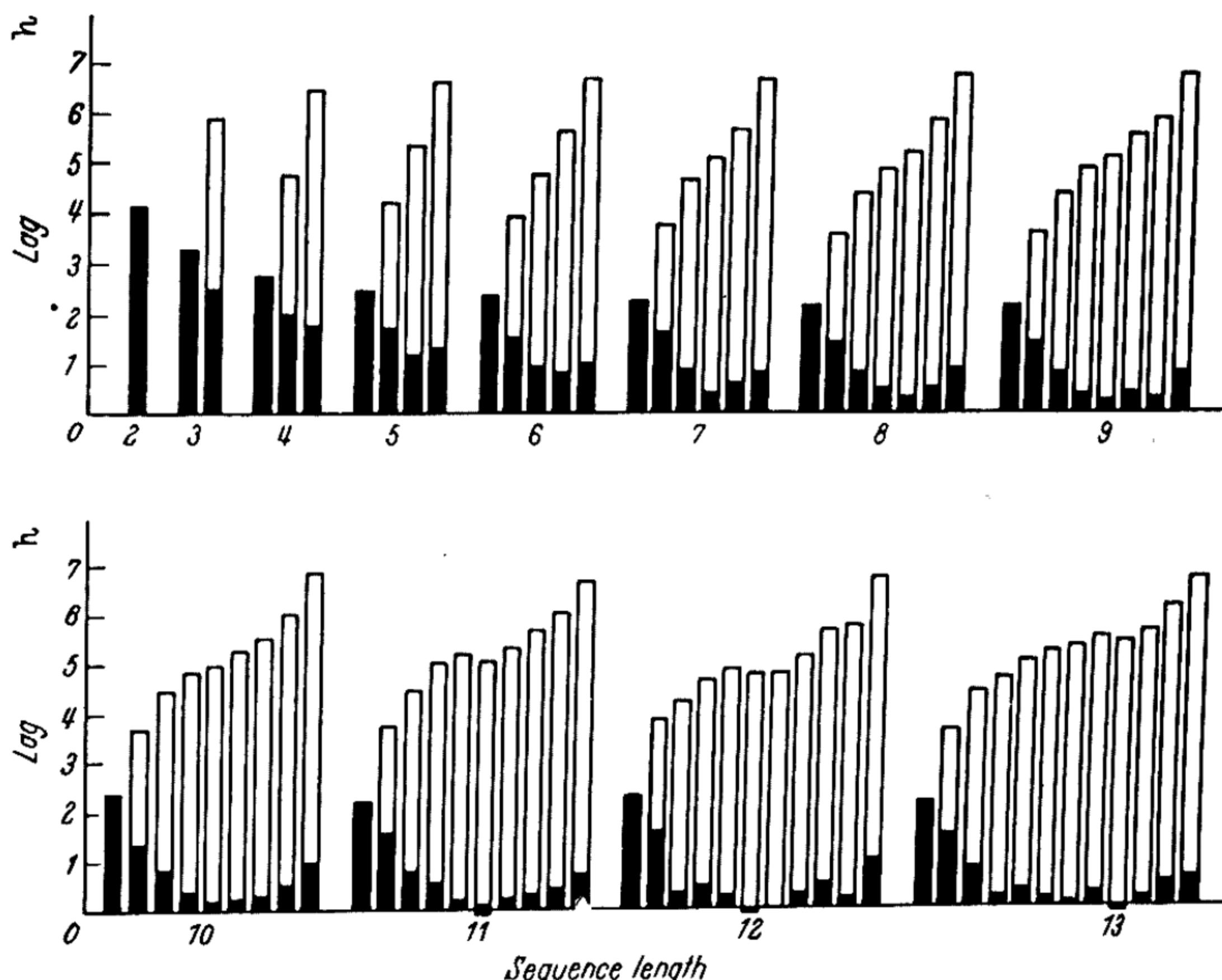


Figure 15.15. Lag in ovulation sequences, 2 to 13 members. Based on data from Heywang (1938).

element of 'discontinuity' into the order of lag values. While these considerations do not constitute evidence that hO_2 is in fact equal to hL_n , they do lend a measure of support to the inference that the *order* of lag relationships existing within and between ovulations may be approximated by the procedures described.

The order of change of some lag components and total lag in ovulation sequences (or cycles) of different lengths is well brought out in *Figure 15.16*. The curves are based on the same data (Heywang) as are *Figures 15.12* and *15.15*. Total lag is seen to increase rather rapidly as sequence length increases from 2 to 6, remaining thereafter fairly constant. Lag at the second place in the sequence (hO_2) decreases gradually as n increases to about 7, and is fairly constant in longer sequences. The minimal value of lag decreases over a greater range, approximating zero only in sequences of 11 or more members

(compare *Figure 15.15*). Mean lag must of course decrease indefinitely, but obviously does so very slowly as sequences increase beyond 8 to 10 members.

Characteristics of the Ovulation Cycle

While the distribution of individual and cumulative lag values differs in oviposition and ovulation sequences, total lag, and therefore mean lag, are unchanged in sequences of the same length. The characteristics of closed cycles containing sequences of a given length are also unchanged, and ovulation frequency is defined exactly as for oviposition sequences, $f = n/(n + 1)$. Actually, of course, the oviposition cycle is merely an expression of the fact that ovulations previously occurred to form a cycle.

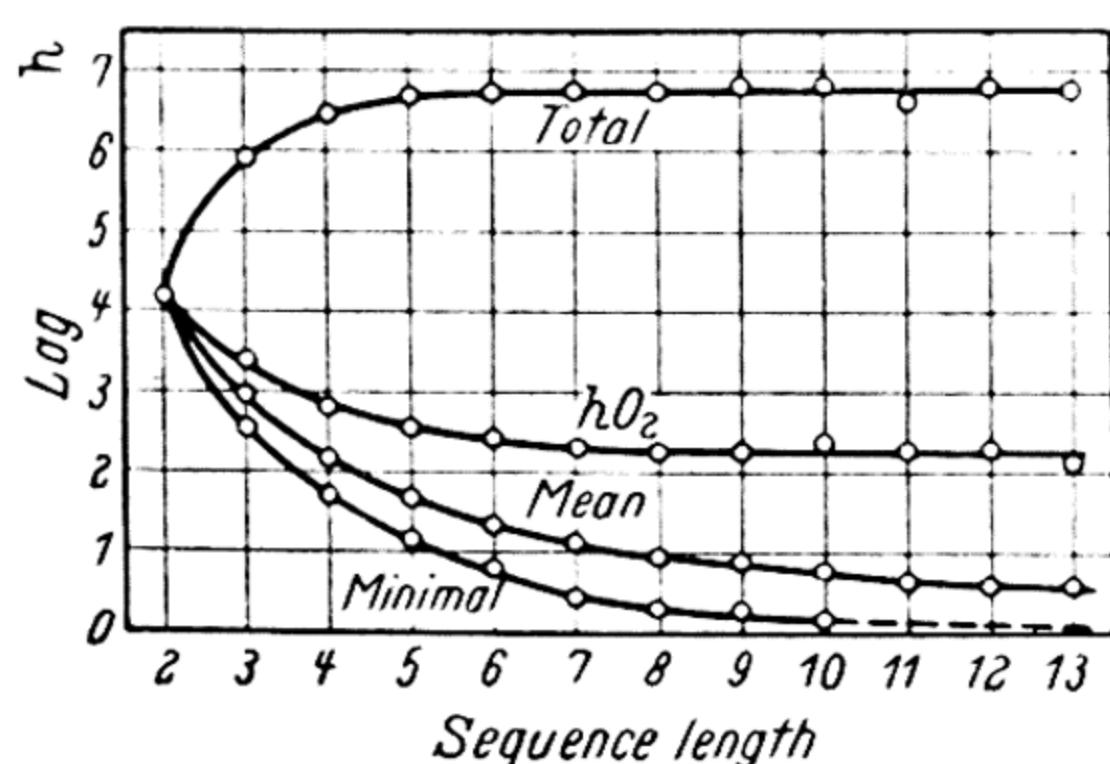


Figure 15.16. The variation of lag at the second place (hO_2), mean lag, total lag and minimal lag with sequence length. Based on data from Heywang (1938).

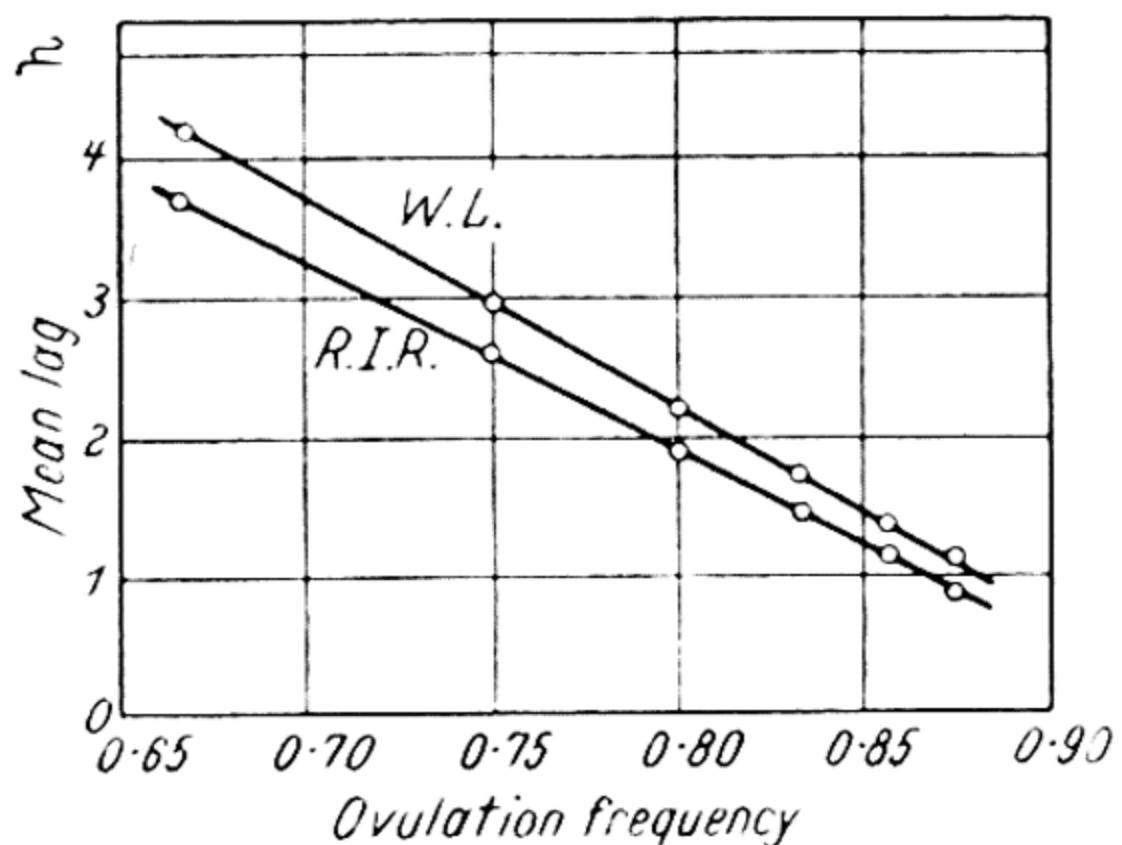


Figure 15.17. Variation of mean lag with ovulation frequency in White Leghorns (W.L.) and Rhode Island Red (R.I.R.) hens. Based on data from Heywang (1938).

An interesting correlation has been noted between mean lag and ovulation frequency. The curve representing mean lag in *Figure 15.16* is obviously hyperbolic (cf. Hays, 1936). If the values of mean lag over the range $n = 2$ to 7 are plotted against ovulation frequency, they are found to fall almost perfectly on a straight line (White Leghorns of *Figure 15.17*). Mean lag values for Rhode Island Reds (Heywang) fall on another straight line of lesser slope. Over the indicated range, mean lag is obviously directly proportional to ovulation frequency. The significance of the indicated relationship is that ovulation frequency, rather than sequence length or cycle length, is the proper measure of differences between closed cycles of varying lengths.

A most important aspect of lag in the ovulation cycle is total lag, which may be written Σh . Total lag sets off the hours of the 24 during which ovulation may occur, and within which it does occur in sequences of given length. By the same token, total lag allows us to define,

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TABLE 15.13

ESTIMATION OF THE INTERVAL BETWEEN C_n AND C_1 OVULATIONS
AND OF THE PERIOD OF LAPSE IN CLOSED CYCLES, WHITE LEGHORN HENS
(Beltsville)

<i>n</i>	Total lag	C_n to C_1 interval	Mean interval	Period of lapse*
2	4.53	43.47	28.53	14.84
3	6.68	41.32	27.34	13.98
4	7.38	40.62	26.46	14.18
5	7.75	40.25	25.94	14.31
6	8.15	39.85	25.63	14.22

* (A convenient approximation, as will appear later.)

as $24 - \Sigma h$, the hours of the 24 during which ovulation does not normally occur. To account for the failure of ovulation to occur during these hours of the 24, particularly in the closed cycle, is among the main objectives of a following section.

One of the most important 'time factors' in the closed ovulation cycle is the interval between C_n ovulation of one sequence (O_3 of *Figure 15.13*) and C_1 ovulation of the succeeding sequence (O_1' of *Figure 15.13*). This interval includes, of course, the single 'day' of no ovulation in the closed cycle. The C_1 ovulation occurs therefore on the second day following C_n ovulation and, in ideally repeated sequences, it is earlier in the day than was the C_n ovulation by the extent of total sequence lag. That is, the interval between C_n and C_1 ovulations is found as $48 - \Sigma h$ hours. Its value is so estimated in Table 15.13 for the same Beltsville Leghorns used in previous tables. For purposes of comparison, mean lengths of intervals between successive ovulations in the sequences are included in Table 15.13; the difference between the C_n to C_1 interval and the mean (sequence) interval is given in the last column of the table. This difference is a rough measure of additional time elapsing between C_n and C_1 ovulations over what might be expected if ovulation had occurred on the day of 'missed' ovulation in accordance with previous (mean) intervals. This difference is therefore an approximate measure of the period of lapse in the ovulation cycle. It is worth noting that one closed cycle is completed and another initiated only because of the occurrence of the period of lapse; as long as ovulation continues on consecutive days, a cycle cannot be completed (see *Figure 15.13*).

FOLLICULAR RESPONSES TO OVULATION-INDUCING HORMONES

The follicles of a sequence or cycle are designated the C_1 , C_2 , . . . , C_n in the order of their normally expected ovulation

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(Table 15.10), and like ovipositions and ovulations, those subsequent to the first or C_1 of the sequence are referred to collectively as C_s follicles (cf. Fraps and Dury, 1943a). In describing any effect of ovulation-inducing hormones in the normal cycle, it is necessary to indicate both the place of the follicle in the cycle and time of its normally expected ovulation. When referring to the C_1 follicle, it is always to be remembered that the interval between C_n and the succeeding C_1 ovulation is considerably greater than are intervals between ovulations within the sequence (Table 15.13 and *Figure 15.13*). In the usual course of events only a single follicle is ovulated on a given day, although exceptions to this rule do occur (see CONRAD and WARREN, 1940).

GONADOTROPHIN-INDUCED OVULATION

Curiously, the first evidence for direct hormonal induction of ovulation in fowls came out of experiments on birds pretreated with pregnant mares' serum (PMS). Following Bates, Lahr and Riddle

TABLE 15.14

TIME OF OVULATION FOLLOWING INTRAVENOUS INJECTION OF A LUTEINIZING PREPARATION, 20 UNITS PER HEN, INTO WHITE LEGHORN HENS PRETREATED WITH PREGNANT MARES' SERUM, 100 UNITS DAILY, THROUGH 8 DAYS

No. of hens	Time of ovulatory injection	Injection to autopsy, hr.	Ovulations per ovulating hen, No.	Injection to ovulations	
				Avg., hr.	Range, hr.
5	8.30 a.m.	7.2	1.5	7.0	6.6-7.2
4	1.00 p.m.	7.1	2.3	6.7	6.3-7.1
3	6.00 "	7.1	3.3	6.9	6.6-7.1
3	9.15 "	7.1	2.7	6.6	6.1-7.0

From Fraps, Riley and Olsen (1942). *Soc. for Exp. Biol. and Med.*

(1935), PMS was administered subcutaneously daily to laying hens to stimulate follicular development. The ovaries of hens so treated for 6 to 11 days carried numerous large, apparently normal follicles, partly in consequence of the fact that PMS, thus administered, interrupts normal ovulation after a day or two. At the end of the period of pretreatment, the birds were given a single intravenous injection of a luteinizing preparation from horse pituitaries (Fraps and Riley, 1942). As many as 7 follicles were caused to ovulate from a single ovary. These experiments were repeated, substantially, to determine the interval between injection of the LH preparation and the occurrence of ovulation (FRAPS, RILEY and OLSEN, 1942). Results are given in Table 15.14; the relatively brief interval from injection to ovulation, 6 to 7 hours, is to be noted. It is of some interest that in all hens in which multiple ovulations occurred in these

two experiments, only a single ovum was picked up by the oviduct. A similar response of FSH pretreated hens to LH preparations was reported by Nalbandov and Card (1946).

The occurrence of multiple ovulations in response to a single intravenous injection in the PMS pretreated hens indicated that a number of follicles had become highly ovulable, and remained so in the absence of the recurrent stimulus for their ovulation. The usual sequential or cyclic order of ovulation was thus no longer apparent. Such responses accordingly could tell us nothing about the behaviour of the single maturing follicle of the sequence.

Premature ovulation of single C_s follicles was soon found to follow the intravenous injection of any of several gonadotrophins (FRAPS, OLSEN and NEHER, 1942). The luteinizing preparation used in the PMS pretreatment experiments proved relatively the most effective. It was of some interest to observe that preparations of PMS, intravenously injected, readily caused premature ovulation, although they interrupt normally occurring ovulation following their subcutaneous administration. At a relatively high injection level (1,200 I.U.),

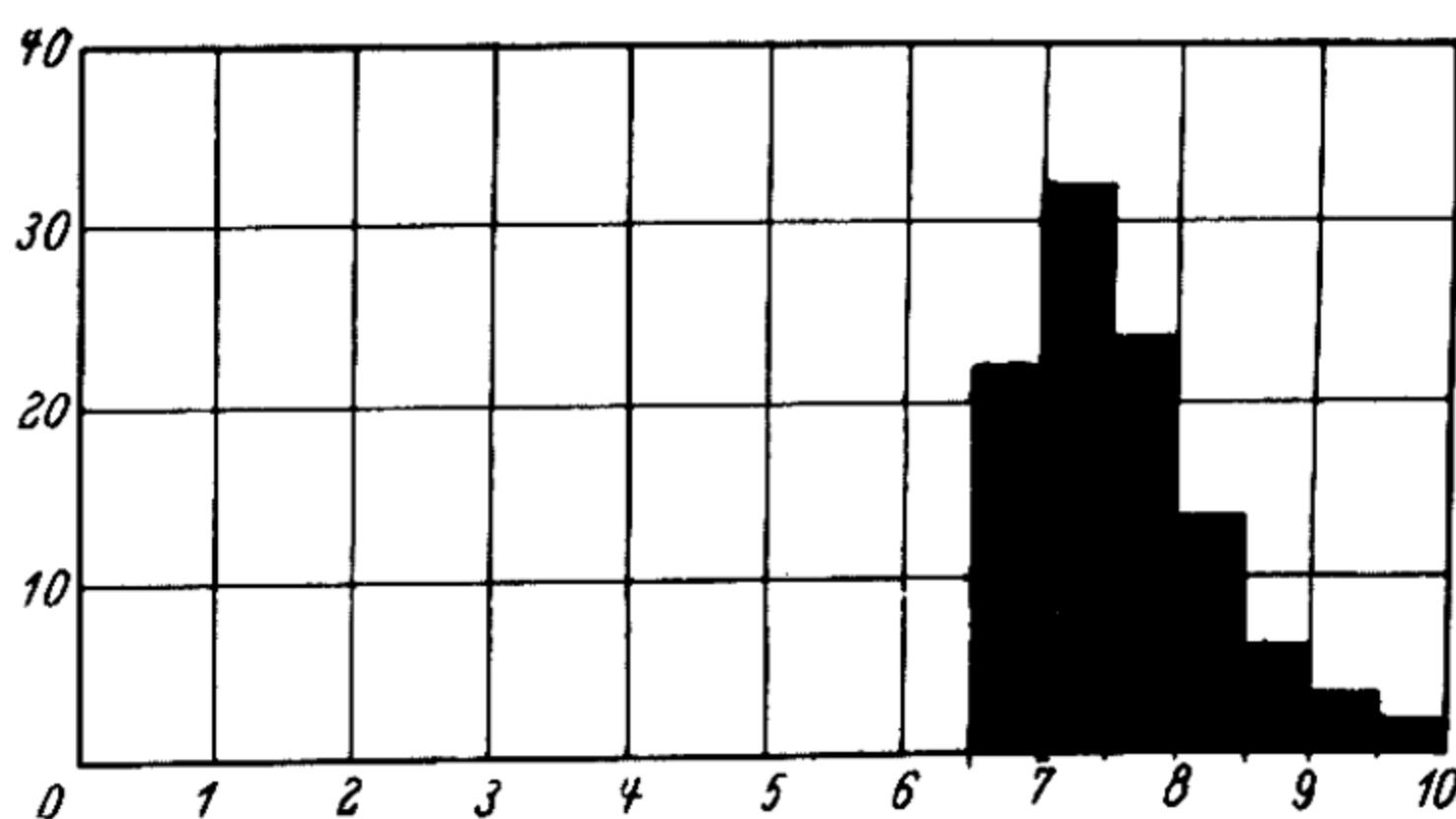


Figure 15.18. Distribution of induced ovulations, non-pretreated hens, in time from injection of ovulatory preparation. Abscissas, time in hours from injection (0 hour); ordinates, percentage of ovulations occurring within indicated 0.5-hour intervals. (From Fraps, Riley and Olsen (1942), by courtesy *Soc. Exp. Biol. med.*)

ovulation of the C_s follicle was caused to occur as much as 17 hours before time of its normally expected occurrence. The proportion of ovulations induced by the same dosage level was found, however, to increase rapidly as the interval between injection and expected ovulation was decreased.

The interval between injection and resulting (premature) ovulation of C_s follicles varied between 6.5 and 10 hours, as can be seen in Figure 15.18 (Fraps, Riley and Olsen, 1942). However, 90 per cent of all C_s ovulations were forced within 6.5-8.5 hours; the greater range in interval between forced C_s ovulations, compared with the interval in PMS pretreated hens, was believed to be due to the highly varying conditions under which ovulations were forced in the

regularly laying hens (Fraps, Riley and Olsen, 1942). Under optimal conditions, including injection for forced ovulation at relatively limited prematurities, the interval from injection to ovulation of C_1 follicles is probably closer to the interval observed in the PMS pretreated hens than is indicated by some of the data of *Figure 15.18*.

Following the work with the C_1 follicle, it was found that the C_1 follicle was much more reactive to ovulation-inducing gonadotrophins, injected at equal hours before expected ovulation, than was any C_2 follicle. FRAPS and DURY (1942) reported that the C_1 follicle could be ovulated prematurely by 8 to 15 hours following the intravenous injection of relatively small quantities of luteinizing preparations. Later, the C_1 follicle was found to be ovulable, following the injection of small quantities of luteinizing preparations from horse or male chicken pituitaries, by 20 to 24 hours before the expected time of ovulation (FRAPS, 1946). The interval between injection (intravenous) and C_1 ovulation was given by Fraps and Dury (1942) as of the same order, approximately 8 hours, as for C_2 follicles. In later work (unpublished), injection of male chicken pituitary preparations some 14 hours before time of expected ovulation was found to force ovulation of the C_1 follicle within as little as 6 hours in some hens, and within 7.5 hours in most birds.

A further examination of the data from the above and other experiments indicated that in the closed cycle, C_1 and C_2 follicles became about equally responsive to ovulation-inducing gonadotrophins at about equal times following the preceding ovulation. In an attempt to demonstrate this relationship more directly, an anterior pituitary preparation (male chicken) was administered at varying times following the preceding ovulation to determine, at least approximately, the level required to cause ovulation in about half (40-60 per cent) of birds in injected groups. All hens were ovulating in 2-member sequences (3-day cycles). Diagnosis of ovulation was based on autopsy of all injected hens except those (with C_1 follicles) injected 29.5 hours following preceding (C_2) ovulation. Results, based upon some 240 autopsied hens, are shown in Table 15.15 (FRAPS, ROTHLCHILD and NEHER, unpublished). The 'best estimate' of the quantity of pituitary powder required to force ovulation is a rough approximation, for only rarely did a given injection yield a result within the desired 40-60 per cent limits. Nevertheless, it is obvious that the reactivity of both the C_1 and the C_2 follicles increases greatly as the interval between preceding ovulation and injection increases from 7 to some 16 or 19 hours. At these latter intervals both follicles exhibit the same order of response to relatively small quantities of injected material. It is worth noting, however, that—assuming a 7.5-hour interval from injection to forced ovulation—the prematurity of forced C_2 ovulation is only 5 or 2 hours for injections made at 16 or 19 hours following

the preceding ovulation, while the corresponding prematurities of forced C_1 ovulation are 20 and 16 hours. The C_1 follicle probably increases somewhat further in reactivity as the interval from preceding ovulation to injection is increased beyond 19 hours (Table 15.15), but this increase is relatively small.

The fact that C_1 and C_2 follicles become highly sensitive to gonadotrophins by about the same interval following the preceding ovulation tells us that the longer interval between C_n and C_1 ovulation (Table

TABLE 15.15

APPROXIMATE QUANTITIES (MG/HEN), MALE CHICKEN ANTERIOR PITUITARY POWDER REQUIRED TO CAUSE OVULATION OF C_1 AND C_2 FOLLICLES IN 50% OF HENS INJECTED INTRAVENOUSLY AT INDICATED HOURS FOLLOWING THE PRECEDING OVULATION ($n=2$ IN ALL SEQUENCES)

Hours from preceding ovulation	'Best estimate' of 50% ovulation level	
	C_1 Follicle	C_2 Follicle
4	>1.00*	>1.00*
7	0.50	0.20
10	0.15	0.15
13	0.05	0.10-0.15
16	0.02	0.02
19	<0.02	<0.02
29.5	ca.0.01	—

* Results at this level were erratic, with death sometimes following injection.

15.13) cannot be attributed to the lack of a normally reactive follicle during the latter hours of this interval, *i.e.* during the period of lapse. This conclusion is confirmed by experiments in which ovulations were forced to occur, over several successive days, as successive additions to a normally completed sequence (NEHER and FRAPS, 1950).

HYPOPHYSIAL CONTROL OF OVULATION

It might reasonably be concluded from the follicular responses to gonadotrophins that ovulation is caused by the release of an ovulation-inducing hormone (OIH) from the anterior pituitary body at a definite interval before actual ovulation. Evidence that this is so came from the results of hypophysectomy of regularly ovulating, mature hens (ROTHCHILD and FRAPS, 1949a). Preliminary work showed that no ovulations subsequently occurred in hens hypophysectomized 10 hours before the expected event, while all hens ovulated following hypophysectomy 2 hours before expected ovulation. Birds were accordingly hypophysectomized at various times between 10 and 2 hours before expected ovulation of C_1 or C_2 follicles. Results are grouped in Table 15.16 in terms of three intervals from hypophysectomy to actual

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or expected ovulation, *viz.* intervals of 4 hours or less, intervals of more than 4 but less than 6, and intervals of more than 6 hours. The percentage of ovulating birds increases as the interval from hypophysectomy to expected (or actual) ovulation decreases. The results indicate also that the most frequently encountered interval between hypophysectomy and either C_1 or C_s ovulation is 4 to 6 hours (average within the interval, very close to 5 hours).

ROTHCHILD and FRAPS (1949a) noted that theoretically the duration of OIH release may be very brief or extend over a considerable period of time. The results of hypophysectomy of normally ovulating hens do not answer this question. For most birds, the interval recorded in Table 15.16 is appreciably less than is the mean interval following the intravenous injection of ovulation-inducing gonadotrophins. The results of hypophysectomy may mean therefore that OIH release

TABLE 15.16

RELATION BETWEEN THE INTERVAL FROM HYPOPHYSECTOMY TO ACTUAL OR EXPECTED OVULATION AND THE PERCENTAGE OF BIRDS OVULATING (SEE TEXT)

Range	Interval: Hypophysectomy to actual or expected ovulations		Total number of birds		Birds ovulating			
	Average				Number		Per cent	
	C_1 ovulations	C_s ovulations	C_1 ovulations	C_s ovulations	C_1 ovulations	C_s ovulations	C_1 ovulations	C_s ovulations
(hours)	(hours)							
2.0–4.0	3.3	3.5	10	11	10	9	100	82
4.2–5.8	5.0	5.1	35	12	21	7	60	58
6.0–10.5	7.2	7.3	74	18	13	4	18	22

Table 16.—From Rothchild and Fraps (1949a). *Endocrinology*.

continues over a considerable period, or that some other hormone secreted by the pituitary is essential for maintenance of the follicle even though the duration of OIH release is limited. Other results bearing on this problem will be considered later. In the meantime it will be convenient to assume that the mean interval between OIH release and ovulation is of the order of 6.5 to 7.5 hours, as is indicated by the results of injection experiments.

Regardless of the absolute length of interval between OIH release and ovulation, the results shown in Table 15.16 indicate that this interval is the same for all members of the sequence. As Rothchild and Fraps (1949a) observed, the successively later hours at which ovulations occur within a clutch are 'thus traceable to successively later releases of ovulating hormone'. This means that lag and intervals in the OIH release sequences are the same as in the corresponding

ovulation sequences. Total lag in any OIH release sequence is thus also the same as in the ovulation sequence; it follows that estimates of the interval between C_n and C_1 ovulations as well as of the period of lapse in this interval in the closed ovulation cycle (Table 15.13) apply equally to the corresponding OIH release cycle. Since an ovulable follicle is 'available' during the period of lapse, and since OIH is not released during the corresponding period in the release cycle, the sources of failure in the mechanism of OIH release are obviously to be sought out in accounting for the period of ovulatory lapse.

Nature of the ovulation-inducing hormone

It has been noted that LH preparations were relatively more effective than others in causing premature ovulation of C_1 follicles. The C_1 follicle was found also to be more responsive to LH preparations from sheep pituitaries; FSH preparations from the same source were effective only when administered at levels sufficiently high to carry appreciable quantities of LH (Fraps and Dury, 1943b). Similarly, the luteinizing fraction prepared from male chicken pituitaries was found to be extremely potent in forcing C_1 ovulation, while other fractions (FSH, growth and adrenotrophic) were effective only to the extent that LH may have been present as a contaminant (FRAPS, FEVOLD and NEHER, 1947). It is of some interest in this connection that RILEY and FRAPS (1942b) placed the male chicken pituitary among types with a relatively high LH content. The ovulation-inducing potency of the male pituitary is some 10 to 12 times that of the pituitary from laying hens and about 8 times that of non-laying females (FRAPS, 1943). The relatively low potency of the pituitary from the ovulating hen is possibly associated both with high oestrogen levels (RILEY and FRAPS, 1942a) and the periodic release of presumably greater quantities than occur in the male or the non-laying female.

In view of the available evidence, ovulation in the hen is probably induced by periodically increased levels of LH in the blood stream. In this sense we may speak of LH as the ovulation-inducing hormone. It should be remembered, however, that in the normally ovulating fowl there is also present in the blood stream a relatively high level of FSH, and we do not know that ovulation can be induced by LH in the absence of FSH (see Hisaw, 1947); nor do we know that the ovulation-inducing hormone (OIH) release consists exclusively of LH.

PROGESTERONE-INDUCED OVULATION

Although DUNHAM and RIDDLE (1942) reported that progesterone failed to cause premature ovulation in pigeons or ring doves, this steroid was found to be highly effective in the induction of ovulation in the hen (Fraps and Dury, 1943a). The route of administration,

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however, proved to be important in connection with the response of C_s (usually C_2) follicles. As can be seen in Table 15.17, the C_1 follicle gave a good response (70.4 per cent ovulations) to the intravenous injection of as little as 0.2 mg. progesterone per hen, and a near maximal response at the 0.5 mg. level. Subcutaneously injected, progesterone was not quite as effective in forcing C_1 ovulations at very low dosages, but caused a high proportion of C_1 ovulations at levels of around 1 mg./hen.

TABLE 15.17

EFFECT OF PROGESTERONE, 4 P.M. INJECTIONS, IN FORCING OVULATION OF OVARIAN FOLLICLES OF THE HEN AT LEAST 6 HOURS PREMATURELY

Injection		Hens with C_1 follicles			Hens with C_s follicles		
		Injected, No.	Ovulating		Injected, No.	Ovulating	
Route	Level, mg	No.	%	No.	No.	%	
Intravenous	0.01	—	—	—	10	0	0
„	0.02	9	1	11.1	20	0	0
„	0.05	13	4	30.8	18	0	0
„	0.20	27	19	70.4	11	0	0
„	0.50	9	8	88.9	6	0	0
„	1.00	10	9	90.0	7	0	0
„	1.5-5.0	—	—	—	8	0	0
„	10.0	17	10	58.8	7	1	14.3
„	15.0-40.0	—	—	—	16	1	6.3
Subcutaneous	0.05	20	0	0	—	—	—
„	0.125	21	4	19.0	9	0	0
„	0.25	29	20	69.0	8	0	0
„	0.50	25	19	76.0	15	11	73.3
„	1.0	19	18	94.7	14	10	71.4
„	2.0	11	10	90.9	7	5	71.4
„	3.0	—	—	—	13	10	76.9
„	5.0	7	7	100.0	11	8	72.7
„	10.0	10	9	90.0	10	5	50.0

Table 17.—From Fraps and Dury (1943). *Soc. Exp. Biol. and Med.*

By the intravenous route, it proved almost impossible to induce premature ovulation of the C_s (or C_2) follicle when progesterone was administered at 4 p.m. (Table 15.17). In contrast, the subcutaneous injection of progesterone at the same hour induced C_2 ovulations in 73 per cent of hens receiving as little as 0.5 mg. This proportion of responses was not appreciably increased as the injection level was increased from 0.5 to 5 mg./hen. Intravenously injected, progesterone is now known to disappear rapidly from the blood stream (HASKINS, 1950; BUTT *et al.*, 1951; EDGAR, 1953). The marked difference in incidence of forced C_2 ovulations with route of injection probably

means that the hormone must act over a sufficiently long time as well as at an effective concentration to force ovulation of this follicle prematurely (cf. Fraps and Dury, 1943a).

Since the interval between 4 p.m. injections and expected C_1 ovulation (approx. 14 hours) was less than that between injections at the same hour and expected C_2 ovulations (approx. 18.5 hours), progesterone was injected at 11 a.m., or 19 hours before expected C_1 ovulation, in order to make a more direct comparison of C_1 and C_2 responses. Intravenously injected at the level of 0.2 mg./hen, the steroid forced C_1 ovulation prematurely in 53 per cent of 17 treated hens; subcutaneously injected at 0.25 mg./hen, 54 per cent of 24 treated hens ovulated prematurely. The differences in response of C_1 and C_2 follicles to intravenously injected progesterone (Table 15.17) cannot be attributed, therefore, to differences in the intervals between times of injection and times of expected ovulation.

It has been pointed out that multiple ovulations are induced promptly by a single intravenous injection of LH into hens pretreated with PMS. Progesterone was found to be completely ineffective, even in dosages up to 40 mg./hen, in the induction of ovulation in similarly pretreated hens. Since subcutaneously injected PMS was known to interrupt normal ovulation after a day or two, the failure of pretreated hens to respond to progesterone prompted an examination of the 'ovulation-inducing' capacities of the anterior pituitary glands from PMS pretreated hens. The potencies of these glands were found to be far below that of glands from the normally ovulating hen. The results of these tests (noted in ROTHCILD and FRAPS, 1949b) led to the supposition that progesterone failed to induce ovulation in the PMS treated hen because the steroid acted on or through the pituitary; the pituitaries of normal hens were believed to carry ample reserves to respond (by whatever mechanism), while the pituitaries of PMS pretreated hens did not.

Subsequently, Rothchild and Fraps (1949b) showed that progesterone failed to induce either C_1 or C_2 ovulations in the hypophysectomized hen. Moreover, it was found that the hypophysis must remain intact for 2 to 4 hours following the injection of progesterone for ovulation to occur in response to injection. These results were believed to afford convincing evidence that progesterone induced premature ovulation in the intact hen by causing the release of ovulation-inducing hormone from the anterior pituitary body, not by any direct action on the mature or ovulable follicle.

The mechanism by which progesterone caused the anterior pituitary body to release OIH was not clarified by the hypophysectomy experiments. Since progesterone disappears rapidly from the blood stream, however, Rothchild and Fraps (1949b) thought it improbable that 2 to 4 hours must elapse between injection of progesterone and the

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release of OIH. It was suggested, rather, that progesterone acted promptly to cause the release of OIH, but that the pituitary must remain intact for some time thereafter for secretion of a hormone required for maintenance of the ovulating follicle.

The interval from steroid injection to ovulation

According to Fraps and Dury (1943a) progesterone injected either intravenously (0.2 to 0.6 mg./hen) or subcutaneously (0.5 to 1.5 mg./hen) forced ovulation of the C_1 follicle within some 7 to 9 hours. Under comparable conditions, the interval from injection (subcutaneous route only) to ovulation of C_1 (or C_2) follicles was found to be of the order of 8 to 11 hours. The time of ovulation was arrived at, in these experiments, by sacrificing hens well after the time of actual ovulation, removing the oviduct, and estimating time of ovulation from place of egg in the magnum.

TABLE 15.18

INTERVAL FROM INJECTION OF STEROIDS TO OVULATION. INJECTIONS AT 4 P.M.,
APPROXIMATELY 14 HOURS BEFORE EXPECTED OVULATION OF C_1 FOLLICLES

Steroid	Quantity mg/hen	Route	Injection to sacrifice			
			7 hours		8 hours	
			Injected, No.	Ovulating, No.	Injected, No.	Ovulating, No.
PGST	0.5	Iv.*	10	1	8	8
	1.0	Sc.*	9	1	8	7
DOCA	1.0	"	8	1	15	13
TST†	1.0	"	11	0	10	0

* Iv., intravenous; Sc., subcutaneous.

† Ovulation occurred in 1 of 9 hens sacrificed 9 hours following injection.

The interval between injection of progesterone (and other steroids) and the resulting C_1 ovulation has recently been ascertained more closely. The steroids were injected (1 mg./hen) at an exact time (near 4 p.m.) and each hen was sacrificed at an exact number of hours thereafter to ascertain the occurrence or failure of occurrence of ovulation at the known hour. Results are recorded in Table 15.18. Practically all hens injected with progesterone, either intravenously or subcutaneously, had ovulated within 8 hours following injection, and only an occasional hen responded in less than 7 hours. Under the conditions of administration noted here, the time required for progesterone to induce C_1 ovulation falls within remarkably narrow limits. For most purposes, the injection-ovulation interval for progesterone may be taken as of the order of 8 hours.

The interval from injection of desoxycorticosterone acetate (DOCA) to ovulation is very similar to that of progesterone (Table 15.18). Testosterone, which is not as effective in forcing ovulation prematurely as progesterone or DOCA, also requires a greater interval (> 9 hours) to produce its effect.

The interval from injection of progesterone to ovulation is not much greater than is the interval from injection of LH to ovulation, and both are greater than the 'apparent' interval from OIH release to ovulation. If, as Rothchild and Fraps (1949b) suggested, the results of hypophysectomy indicate the time before an expected ovulation at which the pituitary becomes 'dispensable' in maintenance of the follicle, these results can tell us nothing as to the *absolute* interval between OIH release and ovulation. They do tell us, however, that C_1 and C_2 follicles behave similarly following either the naturally-induced or progesterone-induced release of OIH.

According to VAN TIENHOVEN (1954), the minimal duration of hypophysial stimulation following the injection of progesterone is of the order of 1.5 hours. Van Tienhoven suggested that stimulation of the pituitary and release of OIH (or LH) proceeded concurrently. If this is so, the interval between onset of OIH release and ovulation should be practically identical with the interval between injection of progesterone and ovulation, *i.e.* about 8 hours. The interval between secretion of sufficient OIH to assure ovulation and actual ovulation would be somewhat less, not more than about 6.5 hours according to van Tienhoven's results. It is interesting that intravenously injected LH preparations force ovulation prematurely within about 6.5–8 hours. While intravenous injection and the natural process of OIH release are obviously not identical, the injection data may be taken as a fair approximation of the interval between 'completed' OIH release and ovulation.

Pituitary competence during the period of lapse

The 'availability' of an ovulable follicle during the period of lapse has been demonstrated, and it was noted that failure of ovulation to occur during these hours must be traced to failure of OIH release. Failure of OIH release to occur during the period of lapse could, of course, have its source in failure on the part of the hypophysis. Good evidence that this is an unlikely possibility was found in the capacity of progesterone to cause OIH release at any time during the period of lapse.

Using hens laying regularly in 3-day cycles ($n = 2$), Neher and Fraps (1950) injected progesterone (or an LH preparation) at times calculated to bring about ovulation of the C_1 follicle of an oncoming sequence as an additional member of the otherwise completed sequence. Actual hours of this first injection were between 4 and 8 a.m. of the

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day after ovulation of the C_2 follicle of the preceding sequence. In effect, this injection served as a substitute for OIH release if the 2-member cycle were to become a 3-member cycle (Table 15.13). Injections subsequent to the first were made at intervals of 24, 26 or 28 hours following the first, and were continued at these intervals until ovulation failed to occur in response to a given injection.

Results are shown in Table 15.19 in terms of 'eggs added' to the otherwise completed 2-egg sequences; the table includes also results based on injection of male chicken anterior pituitary tissue (AP).

TABLE 15.19

EGGS ADDED TO ANTICIPATED 2-EGG CLUTCHES FOLLOWING INJECTION OF MALE CHICKEN ANTERIOR PITUITARY TISSUE (AP) AND PROGESTERONE (Pg)

Group	Hens No.	Injection			Eggs added	
		Hormone	Quantity mg.	Interval hrs.	Per hen No.	Range No.
A	10	AP	1.0	24	2.4	0-5
B	6	AP	1.0	26	3.0	1-5
C	10	Pg.	0.3	24	2.0	0-5
D	10	Pg.	0.6	24	2.5	1-5
E	10	Pg.	0.9	24	2.5	1-4
F*	7*	Pg.	0.3-0.9*	28	4.7 (3.3)†	1-13 (1-7)†

* The birds in this group received 2 injections of 0.3 mg., 2 of 0.6 mg., and all subsequent of 0.9 mg. progesterone.

† Except hen 2477.

From Neher and Fraps (1950). *Endocrinology*.

Progesterone, which had to effect OIH release in order to cause ovulation, is seen to be about as effective as AP, which acted directly on the follicle. The levels of injected progesterone were low (cf. Table 15.17), and even the highest level administered, 0.9 mg., represents no more than about 0.5 mg./kg. It is particularly important to realize that following each consecutively induced OIH release (or ovulation) except the last, a succeeding follicle matured as in the normal sequence. It is interesting to note also that when progesterone was injected at 28-hour intervals (group F of Table 15.19), OIH release (and ovulation) took place at periods throughout the period of lapse (Table 15.13). For the 24-hour intervals (groups C, D and E), OIH release (and ovulation) were induced on consecutive days at or near onset of the period of lapse. As we have seen earlier, a 24 hour interval (lag = 0) is normally attained only in lengthy sequences.

These results, together with other observations noted by Neher and Fraps, demonstrate that the anterior pituitary gland is capable of secreting OIH in quantities adequate for ovulation at any time during

the period of lapse. In a word, pituitary competence parallels ovulability of the maturing follicle, and in the closed cycle, both the pituitary and the C_1 follicle are capable of normal function and response throughout all (or most) of the period of lapse. Since neither of these factors apparently can be invoked to explain the appearance of the period of lapse, it seems necessary to look to the neurohumoral mechanism which is believed to control pituitary response (OIH release) to the 'feed-back' endocrine from the ovary for an explanation. Before doing so, however, it will be helpful to examine a little further the relations existing between OIH release and follicular maturation sequences in the normal closed cycle.

RELATIONS BETWEEN OIH RELEASE AND FOLLICULAR MATURATION

The timing of OIH release and follicular maturation is represented schematically in the same figure (*Figure 15.13*) previously referred to in discussing ovulation-oviposition relationships. So far as ovulation and oviposition were concerned, the ordinary astronomical day served well enough as the cycle day. For present purposes, successive days of the cycle are more conveniently seen in terms of the hours 0-24, 24-48, 48-72 and 72-96 indicated at the top of the diagram. The complete cycle ends with hour 96, which is therefore also zero hour of day 1 of a succeeding cycle. The last day of a preceding cycle (hours 72-96, appearing as 72-0) is also included in the figure. Corresponding events in the preceding, the complete, and the succeeding cycles are assumed to occur at the same times of day.

The onset of each cycle day is understood to be the same as the mean earliest hour in the normal day at which OIH release may occur in cycles of maximal length. This is estimated to be about 11 p.m. under conditions obtaining at Beltsville (White Leghorn hens). The mean latest hour at which OIH release may be expected is around 8 a.m., or hour 9 in the cycle day. The solid bar through the remaining 15 hours of each cycle day marks off the hours during which OIH release never normally occurs. Each day of the OIH release cycle is therefore divided into a 'release' period, actual or potential, and a period of 'lapse'. These are denoted p and q respectively within the hours 72-96 (day 4) of the cycle.

The releases of OIH on consecutive days of the 4-day cycle are represented by R_1 , R_2 and R_3 . There is, of course, no release on day 4, the last day of the cycle, but the first release of the succeeding cycle, R_1' , occurs shortly after onset of the first day, at the same time of day, that is, as did R_1 .

In *Figure 15.13*, the second OIH release of the cycle, R_2 , is seen to occur later in the release period of the second cycle day than did R_1 in the release period of the first cycle day. The retardation in time

of occurrence of R_2 is of course its lag with respect to time of R_1 , and is indicated by hR_2 . Similarly, R_3 takes place later in the release period of the third cycle day than did R_2 in the same period of the second day; lag in the timing of R_3 (relative to R_2) is shown as hR_3 . Since the interval between OIH release and ovulation is—or is understood here to be—the same at all places in the sequence, $hR_2 = hO_2$, and $hR_3 = hO_3$.

On day 4 (hours 72–96 of *Figure 15.13*), OIH release fails to occur either during the usual release period (p), or during the period of lapse (q). If the conditions determining lag at R_3 (or the interval R_2 to R_3) continued to operate through the cycle, OIH release should occur at about the time indicated by Q on day 4. However, since release never occurs during the period of lapse, any OIH release 'expected' at the time of Q can take place only at or following onset of the usual release period on the day thereafter.

In describing the cycle of OIH releases, it was taken for granted that an ovulable follicle was present at the time of each successive release. The ovulating follicles of the cycle are denoted C_1 , C_2 , . . ., C_n , in keeping with the designation of OIH releases as R_1 , R_2 , . . ., R_n , and of the corresponding ovulations as O_1 , O_2 , . . ., O_n . The attainment of substantially equal degrees of ovulability by successive follicles is represented by the curves M_1 , M_2 , etc., of *Figure 15.13*. Here the ascending limb of each curve represents (however diagrammatically) increasing ovulability. The curves are shown as becoming asymptotic simply to indicate the attainment of what might be called a minimal ovulability, the capacity, that is, to respond to normal OIH release at any place in the cycle. Actually, ovulability may continue to increase (as for example in the C_1 follicle) in the sense that the level of injected LH required to force ovulation continues to decrease as long as the follicle remains unovulated after having attained to 'minimal' ovulability. For the present, this is unimportant.

As can be seen in *Figure 15.13*, the follicles attaining ovulability (or maturing) on successive days are the C_2 , C_3 and C_1' ; these constitute the maturation sequence. The sequence of responding follicles (C_1 , C_2 , C_3) matured therefore as the terminal member of a preceding maturation sequence (corresponding to M_1 of *Figure 15.13*) and the first two members of the succeeding maturation sequence. As was pointed out elsewhere (Fraps, 1954c), the sequence of maturing follicles is thus not 'commensurate' with the sequence of ovulating follicles, *i.e.* with the sequence of OIH releases. The reason that the two orders of sequences cannot be so rests in the fact that the terminal member of a maturation sequence must become the first member of the ovulating sequence, of the sequence, that is, responding to the usual sequence of OIH releases (R_1 , R_2 , . . ., R_n).

The essential relationships between the sequences of maturing follicles and of OIH release for ovulation of these follicles are perhaps more clearly seen in *Figure 15.19*. Events of the 4-day cycle of *Figure 15.13* are included under ' $n = 3$ '. As in *Figure 15.13*, the cycle day is divided into a release period, during which OIH release may occur, and the period of lapse, Q during which it does not. The cycle day is understood to be repeated for each day on which OIH release occurs ($n = 3$) and on the day thereafter. On day 1, the first OIH release of the cycle, R_1 , acts on the C_1 follicle, which thus becomes the first follicle of the ovulating sequence; this follicle matured, it will be remembered, as the terminal member of the preceding maturation sequence. On day 2, the second OIH release, R_2 , acts on the C_2 ,

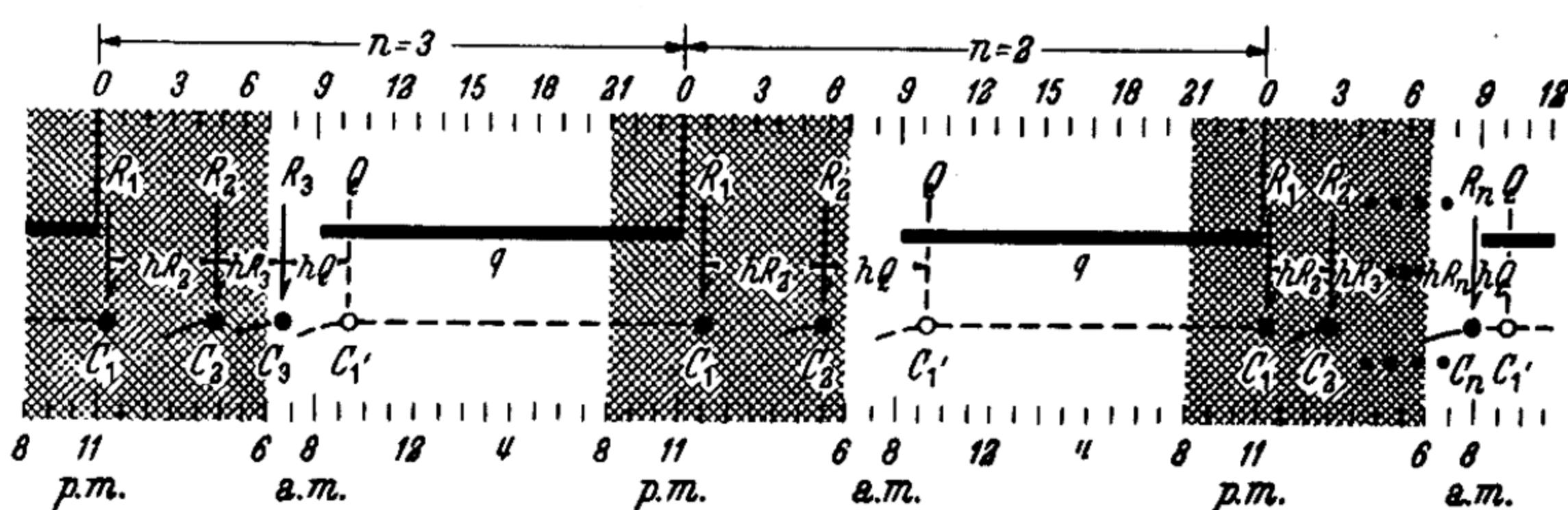


Figure 15.19. The relationships between OIH release and follicular maturation in closed cycles.

follicle of the ovulating sequence, which is, however, the first member of the maturation sequence. The second member of the maturation sequence thereafter is ovulated, in response to R_3 , as the third member of the ovulating sequence. This completes both the OIH release and the responding (ovulating) follicular sequences. But a third follicle now matures, attaining ovulability at about the time of Q on day 4 of the cycle; this is the third, and where $n = 3$, the terminal member of the maturation sequence. In *Figure 15.19*, it becomes the first ovulating member of the succeeding 3-day cycle ($n = 2$). In this cycle the ovulating follicular sequence consists of the C_1 and the C_2 , the maturation sequence of the C_2 and the C_1' . The C_1' follicle of the 3-day cycle is seen to become the C_1 follicle in a cycle of indefinite length. The ovulating follicular sequence is described here as

$$C_1, C_2, \dots, C_n,$$

and the corresponding maturation sequence as

$$C_2, C_3, \dots, C_n, C_1',$$

where the terminal member, C_1' , as in the foregoing cycles of *Figure 15.19*, attains to ovulability at about the time of Q on the last day of the cycle.

The foregoing discussion of relationships between OIH release and ovulation is based on the supposition that each follicle in a cycle becomes equally ovulable at about the same time following the preceding OIH release. But this is the same as saying that each 'curve' of increasing follicular ovulability is displaced, in time of day, by the extent of lag at the preceding OIH release. There is no lag at the first OIH release, hence no displacement is involved in the time course of C_2 maturation (M_2 of *Figure 15.13*). But the lag associated with R_2 , the second OIH release in the sequence, displaces the M_3 curve by the extent of lag at R_3 (*i.e.* by hR_3 hours). This displacement of maturation curves, and thus in times of attainment of minimal ovulability with respect to lag at the preceding OIH release, is seen more directly in *Figure 15.19*.

One other important relationship, already emphasized in connection with the failure of OIH release to occur during the period of lapse, is that maturation of the first follicle of the succeeding sequence (M_2' of *Figure 15.13*) is correspondingly delayed. That this delay or postponement in follicular maturation results (directly or indirectly) from failure of OIH release to occur during the period of lapse is shown by the fact that if ovulation of the C_1' follicle be forced by injection of LH or progesterone at about the time of Q , the C_2' follicle also matures 'prematurely' (Neher and Fraps, 1950). Furthermore, if the OIH release for terminal ovulation in a 3-day cycle ($n = 2$) is delayed, as with oestrogen (Fraps, 1954a), the C_1' follicle fails to mature until after the delayed OIH release takes place. Some stimulus associated with OIH release, or with consequent changes in the ovulating follicle, is apparently required to initiate maturation of the next due follicle in the closed cycle.

NEUROHUMORAL CONTROL OF PITUITARY FUNCTION

The conditions under which the period of lapse occurs in all closed cycles indicates the existence of an intermediary apparatus which serves to permit, or to prevent, ovarian (or follicular) activation of the hypophysis during restricted hours of the 24. A considerable body of evidence justifies the view that nervous factors are involved in the mechanism of OIH release. There is no evidence for direct innervation of the anterior pituitary lobe of the chicken (DRAGER, 1945). Neural control of the hypophysis of the hen is thus most probably effected over vascular pathways by humoral agents which originate in the hypothalamus, as in the mammal (HARRIS, 1948, 1952; GREEN, 1951; BENOIT and ASSENMACHER, 1953; MARKEE, EVERETT and SAWYER, 1952). But in so far as timing of response is in question, as in the successive releases of OIH in a sequence, the nervous or 'neural' component of the mechanism is obviously of primary importance.

NEURAL FACTORS IN OIH RELEASE

In those mammalian species which ovulate in response to mating (e.g. the rabbit), the nervous system has been recognized for some years as an essential link in the release of LH from the pituitary for ovulation. In those species which normally ovulate independently of the mating-reflex, the so-called spontaneous ovulators, the discharge of LH for ovulation is now believed to depend upon a neurohumoral mechanism essentially like that found in the rabbit; but whereas the nervous component of this mechanism is reflexly 'excited' by mating in the rabbit, it is called into play, in the spontaneously ovulating forms (e.g. the rat), by an ovarian hormone, presumably oestrogen (Hisaw, 1947), although in some species this role has been assigned to progesterone (NALBANDOV, 1953b). In the rat, at least, and possibly in other spontaneously ovulating species, the 'neural component of the LH release apparatus' also exhibits diurnal periodicity (or rhythmicity) in sensitivity to the ovarian hormone. Evidence for these conclusions has been reviewed and discussed by EVERETT (1952), Markee, Everett and Sawyer (1952) and EVERETT and SAWYER (1950).

A number of recent reports indicate that the OIH release mechanism of the hen includes a neural component, although this component appears to differ in some respects from that of the rat. Most work on the participation of nervous factors in naturally occurring OIH release has been paralleled by experiments based on the supposition that progesterone-induced OIH release also operated over similar pathways. Evidence bearing on neural control of the natural and induced processes may therefore be considered together.

The injection of any of a number of barbiturates was shown by Everett and Sawyer (1950) to block the release of LH for ovulation in the rat. Usually, if LH release was prevented on one day, it occurred 24 hours later. Everett and Sawyer used Nembutal (pentobarbital sodium) extensively, since its duration of effect was well adapted to suppression of the relatively short period of high sensitivity in the neural apparatus of the rat. Progesterone-induced LH release was also blocked by Nembutal in rats with 5-day cycles (EVERETT, 1951).

In the hen, Bastian and Zarrow (1952) found Nembutal to be incapable of blocking naturally occurring OIH release, even when narcosis was maintained for as long as 12 hours. Nembutal also proved ineffectual in suppressing the LH release induced by progesterone (1 mg./hen, injected intramuscularly).

Working along similar lines, FRAPS and CASE (1953) encountered a surprising diversity of responses to different barbiturates. When administered at 4 p.m. for effect on C_1 follicles, Dial (diallylbarbituric acid), Ipral calcium (probarbital calcium) and Nembutal induced ovulation prematurely in a small but significant proportion of injected

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hens. Moreover, Dial and Nembutal (Ipral was not used) were found to enhance rather than to suppress the ovulation-inducing tendency of progesterone injected at very low dosages (0.1 mg./hen). Some results are reproduced in Table 15.20.

In contrast with the tendency of these barbiturates to facilitate ovulation, phenobarbital sodium, injected under identical conditions, never induced ovulation prematurely; nor did it suppress, to any

TABLE 15.20

ENHANCING ACTION OF PROGESTERONE WITH DIAL AND WITH NEMBUTAL
(From Fraps and Case (1953), by courtesy *Soc. Exp. Biol. Med.*)

Injections	Hens Injected, No.	Premature Ovulations	
		No.	%
Progesterone (0.1 mg/hen)	23	1	4
Dial (100 mg/kg)	16	3	19
Dial + Progesterone	21	12	57
Nembutal (60 mg/kg)	15	2	13
Nembutal + Progesterone	20	6	30

TABLE 15.21

STEROID-INDUCED OVULATION AND ITS BLOCKADE BY PHENOBARBITAL SODIUM.
THE STEROIDS WERE INJECTED AT THE LEVEL OF 1 MG/HEN IN ALL TESTS

Treatment	Hens injected, No.	Hens ovulating	
		No.	%
Progesterone (PGST)*	19	18	95
Phenobarbital + PGST	33	3	9
Desoxycorticosterone Acetate (DOCA)	17	15	87
Phenobarbital + DOCA	22	5	23
Testosterone (TST)	32	13	41
Phenobarbital + TST	28	4	14

* Progesterone controls from Fraps and Dury (1943a).

significant extent, the occurrence of normally expected C_1 ovulations following injection at 4 p.m. (Fraps and Case, 1953), or at later hours. It does, however, suppress some proportion (40–50 per cent) of C_2 ovulations, even when injected as late as 9 hours before the expected event (FRAPS and CONNER, unpublished). Despite its failure to block OIH release for naturally occurring C_1 ovulation, phenobarbital proved highly effective in suppressing progesterone-induced (C_1) ovulation

when the steroid was injected (1 mg./hen) some 30 to 40 minutes following the administration of the barbiturate (Fraps, 1953, and Table 15.21).

As has been noted elsewhere (Fraps, 1954a), the mere diversity of responses to differing barbiturates constitutes good evidence that the mechanism of OIH release in the hen includes a neural component. The 'neural component' involved directly in OIH release probably resides in the hypothalamus, but influences from other centres may conceivably play a part in determining the final response of the hypothalamus itself (Harris, 1952). We know little or nothing of actual relationships in the bird; it is at least conceivable, however, that different barbiturates might have differing effects in a complex 'neural component', but very difficult to see how such diverse effects could be explained as direct actions on the anterior pituitary body.

Apart from the barbiturates, other nervous 'blocking agents' have been reported to prevent ovulation in the hen under conditions which imply suppression of the neural component in the mechanism of OIH release. ZARROW and BASTIAN (1953) found that both adrenolytic (SKF-501) and parasympatholytic (atropine sulphate) drugs blocked naturally-occurring and progesterone-induced ovulation of the C_1 follicle. The blocking actions of atropine and SKF-501 are believed to indicate that the neural mechanism may have both adrenergic and cholinergic components. The authors suggest that a neural link, possibly similar to that of the rabbit and rat, must be present in the mechanism controlling ovulation in the hen.

In view of the capacity of Dibenamine to block LH release in both the rabbit and the rat (Markee *et al*, 1952), VAN TIENHOVEN, NALBANDOV and NORTON (1954) investigated the action of this drug in the hen. Dibenamine was found to block both spontaneous and progesterone-induced C_1 ovulation. The inhibition of spontaneous ovulation was believed to indicate that the drug acted through a mechanism similar to that postulated in mammals, that is, by blocking an adrenergic component in the LH release apparatus.

Dibenamine was found by van Tienhoven *et al* to block spontaneous ovulation in increasing proportions as the interval from injection to expected ovulation was increased from 6 to 10 hours; at 12 hours before expected ovulation it was much less effective than when injected either at 10 or at 14 hours (Table 15.22). The low incidence of blockade observed at 12 hours was believed to represent a real phenomenon, but its cause was not identified.

The fact that Dibenamine blockade is more effective at 14 hours than at 8 or 10 hours before expected ovulation (Table 15.22) led van Tienhoven *et al* to suggest that the 'stimulus for LH release and hence ovulation takes place about 14 hours prior to follicle rupture'. While recognizing that LH release occurs in 50 per cent of their birds some

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8 hours before ovulation, the longer interval (14 hours) is apparently believed to represent the more typical situation.

From experiments of quite a different character, HUSTON and NALBANDOV (1953) have also adduced evidence that nervous factors are involved in LH (OIH) release in the hen. The presence of an irritant, in most cases a loop of thread, in the magnum of the oviduct was found to suppress ovulation for as long as 20–25 days without reduction in size of ovary, oviduct or comb. The ovary frequently carried more than a single follicle of ovulatory size, and these appeared to be entirely normal, without signs of atresia. The condition of the ovary, oviduct and comb suggested that the oviducal irritant did not interfere with the secretion of FSH, or of LH at a low but steady rate.

TABLE 15.22

INCIDENCE OF BLOCKADE OF OVULATION WITH DIBENAMINE ADMINISTERED
INTRAVENOUSLY AT VARIOUS INTERVALS BEFORE EXPECTED OVULATION

Dibenamine dose mg/kg	Time before expected ovulation hours	No. of birds	No. of birds ovulated	No. of birds failing to ovulate	Percentage blocked
30	4	7	7	0	0
30	6	12	9	3	25.0
30	8	12	6	6	50.0
30	10	14	6	8	57.1
30	12	16	13*	3	18.7
30	14	16	2	14	87.5
—	8	13	12	1†	—

* Three birds ovulated about 4 hours after expected time of ovulation.

† This bird ovulated 24 hours after the expected time. This was not considered as a 'blocked' ovulation.

From van Tienhoven, Nalbandov and Norton (1954). *Endocrinology*.

The interruption of ovulation, however, was interpreted to mean that the irritant prevented, over nervous pathways, appearance of the 'ovulatory peaks' in LH secretion (or OIH release) for ovulation (Huston and Nalbandov, 1953; Nalbandov, 1953a). The observations of Huston and Nalbandov were confirmed by VAN TIENHOVEN (1953) who noted also quantitative differences in the suppressing action of the loop in different regions of the magnum; the effect increased with increasing distance from the infundibulum, and was greater in the isthmus than in the magnum.

The results of the foregoing experiments led Nalbandov (1953a) to advance two generalizations regarding the mechanism of ovulation: (i) Like FSH, LH is also assumed to be secreted at a low but steady rate; over and above this basic level, the pituitary periodically releases ovulation-inducing quantities of LH. (ii) The presence of an egg in

the magnum (or isthmus) neurogenically suppresses the ovulatory peaks of LH secretion; when the egg clears the magnum (or isthmus), LH is secreted in quantities sufficient to effect the next ovulation. Nalbandov recognizes certain limitations of this theory, the most important of which is that it does not explain the mechanism of LH release for C_1 ovulation.

THE EXCITATION CYCLE

The author has recently proposed one possible scheme by which periodic excitation of a neural component in the OIH release mechanism may account for timing in the closed cycle (Fraps, 1954a, b). This has been referred to as the 'excitation cycle'. Excitation in this sense is presumably a definitely timed 'event', or at least will be considered so here. The duration of neurohumoral activation is another matter.

It was assumed that excitation, in cycles of given length, preceded each ovulation by a constant interval. It follows that successive excitations (in excitation cycles) stand in the same relationship to each other as do successive ovulations in corresponding ovulation cycles. Thus the lag relationships shown in *Figure 15.13*, or in different form in *Figure 15.19*, apply equally to relative timing in corresponding excitation sequences or cycles. In absolute terms, the interval from excitation to ovulation was taken as of the order of 8 hours, an estimate based on the time elapsing from injection of progesterone to ovulation.

The ovarian hormone exciting the neural apparatus was designated the excitation hormone; its nature is considered later. In closed cycles of given length, blood levels of excitation hormone associated with follicles maturing on successive days were assumed to be substantially the same at equal times following the preceding OIH release. This assumption is based on the order of follicular maturation already discussed. It follows that each 'curve' of increasing hormone concentrations beyond that associated with the first follicle of a (follicular) sequence is displaced, in time of day, by the extent of lag at the preceding OIH release.

The neural apparatus was postulated to exhibit diurnal periodicity in its sensitivity to the excitation hormone. Thresholds of response, a more convenient notation, represent the inverse of sensitivity or excitability in the neural component of the OIH release mechanism (cf. Everett, 1952).

The essential relationships between excitation hormone concentrations and diurnally variable threshold requirements in the neural apparatus are shown for a 7-day cycle in *Figure 15.20*. In the hypothetical ovulation cycle on which the *Figure* is based, it was assumed that C_1 ovulation occurred at 6 a.m., the C_6 ovulation at about 2 p.m., and that lag followed the order (not the absolute values) seen in the

6-member sequence of *Figure 15.15*. Since excitation precedes ovulation by some 8 hours, zero hour and hour 24 of the cycle day (*Figure 15.20*) correspond to approximately 10 p.m.

The curve passing through E_1, E_2, \dots, E_6 and E'_1 describes the diurnally recurrent variation in neural thresholds through the cycle day. This curve is understood to be repeated each day of the cycle. Ordinates to the curve of neural thresholds measure hormone concentrations required for excitation.

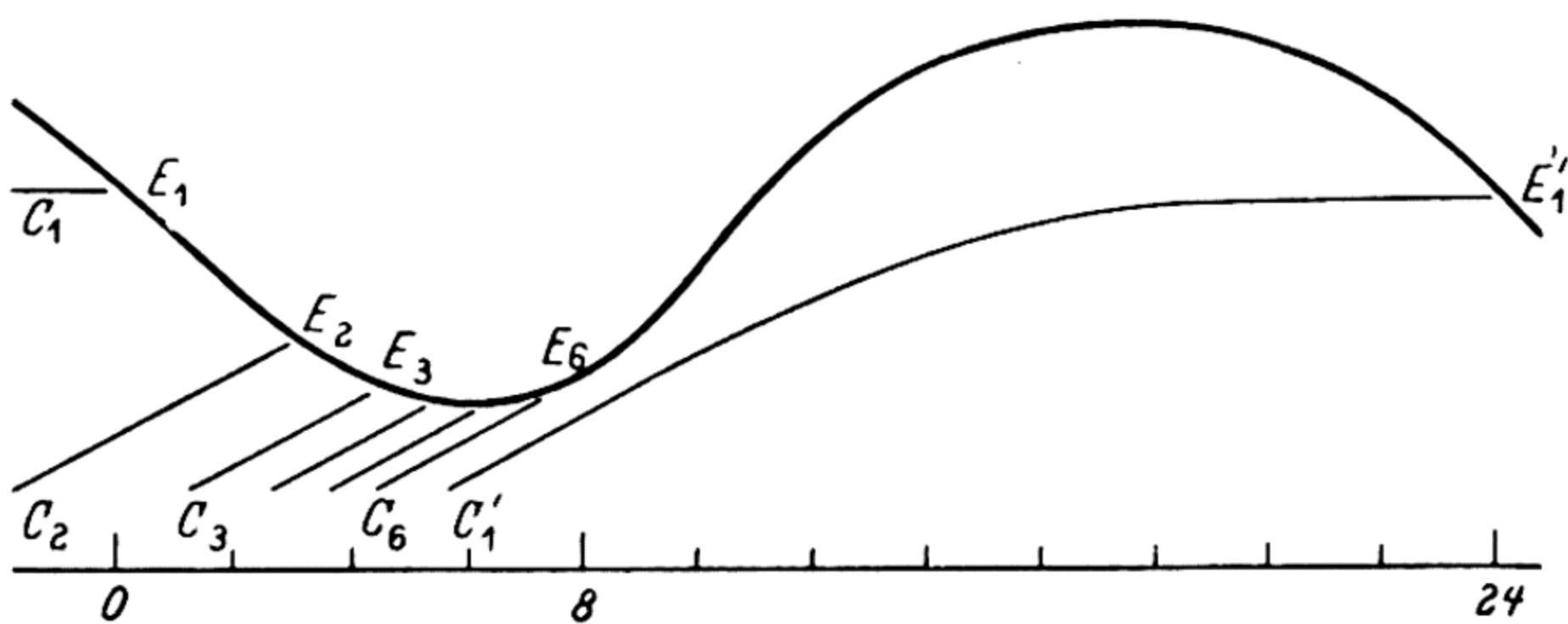


Figure 15.20. Relationships between excitation hormone concentrations and thresholds of response in a 7-day cycle ($n=6$). Abscissas represent hours of the cycle day (0-24), where hour 0 (or 24) corresponds to about 10 p.m., and hour 8 to about 6 a.m., for conditions noted in the text. Excitation for OIH release may occur within hours 0-8, does not occur between hours 8-24. The heavy curve through $E_1, E_2, E_3, \dots, E_6$ and E'_1 represents diurnally recurrent neural thresholds. Ordinates to this curve (not shown numerically) measure the levels of excitation hormone required to effect response of the neural component of the OIH release mechanism. The curves $C_1, C_2, C_3, \dots, C_6, C'_1$ indicate excitation hormone concentrations associated with follicles of the same designation. As these concentrations reach threshold values on successive days, excitations $E_1, E_2, E_3, \dots, E_6$ take place. Hormone levels associated with the C'_1 follicle do not reach threshold values on day 7 of the cycle, hence excitation can only occur at onset of the following day to initiate a new cycle. The displacement of excitation hormone curves on successive days of the cycle is described in the text. (From Fraps (1954a), slightly modified; by courtesy *Proc. Nat. Acad. Sci.*)

Curves C_1, C_2, \dots, C_6 and C'_1 represent terminal excitation hormone concentrations associated with follicles of the same designations. The first excitation of the cycle, E_1 , occurs at a high threshold value (to be clarified presently). Following E_1 (or the first OIH release of the cycle), secretion of excitation hormone is initiated by the C_2 follicle; on day 2 of the cycle the excitation curve C_2 reaches threshold values and causes the second excitation, E_2 . The second excitation, E_2 occurs later in the day than did E_1 , thus defining lag, hE_2 and thus also lag at the second OIH release, hR_2 . The curve C_3 , representing excitation hormone secretion by the C_3 follicle, is displaced in time of day by the extent of lag at E_2 (or R_2). This displacement results in the occurrence of excitation E_3 still later on day 3,

which in turn displaces curve C_4 by the extent of lag at E_3 , or at the corresponding OIH release, R_3 . Successive excitations through the cycle are realized similarly.

The C_1' curve of *Figure 15.20* is of special interest. Like each of the preceding curves except the C_2 (which is the *first* of the maturation sequence), the C_1' curve is displaced by the extent of lag at the preceding excitation, in this case lag at E_6 . This displacement is sufficient to preclude the attainment of threshold values on the day following E_6 , and thus through the period of lapse. Excitation hormone concentrations associated with the C_1' follicle are shown, however, to increase through most or all of the period of lapse. With the reappearance of the diurnally recurrent decrease in neural thresholds, excitation E_1' may thus occur at higher absolute thresholds than elsewhere in the cycle. The first excitation, E_1 , of the complete cycle represented in *Figure 15.20*, is understood to have taken place under the same conditions as did E_1' .

The restriction of OIH release to a relatively limited part of the 24 hours, the failure of OIH release to occur during the period of lapse, and the order of lag exhibited in the OIH release sequences are all quite easily accounted for in terms of the relationships represented in *Figure 15.20*. Nevertheless, this is a highly formal representation, and some of the assumptions on which it is based may call for revision in the future. For example, displacement of excitation hormone curves may not be as closely related to lag at the preceding OIH release as has been assumed, but found to vary for other reasons through the sequence. Again, the disturbing failure in blocking normally expected OIH release with Nembutal, and the advancement of time of C_1 ovulation with certain barbiturates, are certainly indicative of complexities in the 'neural component' apparently not encountered in the rat. For these and other reasons the 'excitation cycle' is to be considered as a formulation of possible rather than of proven relationships; it does have the merit of pointing up some specific problems. A few of these are discussed briefly in the following pages.

The Excitation Hormone

There is general agreement that the level of pituitary function is regulated to a large extent by endocrines from the target organs. In the control of OIH release, the 'feed-back' hormone must be secreted by the ovary or a part of the ovary, *e.g.* the maturing follicle. The 'regulatory' ovarian hormone for LH release for ovulation in the rat (and perhaps in mammals generally) is believed to be oestrogen, as has already been noted, though for some species this has been questioned (Nalbandov, 1953b).

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A similar role of oestrogen in the hen seems unlikely. In the ring-dove (Dunham and Riddle, 1942) and in the hen (Fraps, 1954a), oestradiol benzoate delays the second ovulation of the clutch or sequence. The period of delay is typically 24 hours in the dove; in the hen, the delayed C_2 follicle subsequently behaves like a normal C_1 follicle, and the period of delay is thus of the order (when $n = 2$) of 19–20 hours. ROTHCCHILD and FRAPS (1947) had observed earlier the typical 19–20 hour delay to follow abdominal operations. In both instances, the delay in C_2 ovulation and its subsequent occurrence as a typical C_1 ovulation indicate interference with some mechanism exhibiting diurnally recurrent periodicity. The results of oestradiol benzoate administration, specifically, led to the view that this steroid decreased sensitivity of the postulated neural component of the OIH release mechanism (Fraps, 1954a). If this view is correct, it is difficult to see how oestrogen can serve as the excitation hormone.

Evidence favouring the view that the excitation hormone may be a progestin, if not progesterone itself, has been discussed recently (Fraps, 1954c). The capacity of progesterone to induce OIH release, and evidence that it does so through a neural mechanism, have been noted in the present paper. It is significant also that progesterone (or an equivalent progestin) has been demonstrated by the method of Hooker and Forbes (1947) to occur in the blood stream of the laying hen (Fraps, Hooker and Forbes, 1948), as well as in the plasma of non-laying hens and cocks, but not of capons (Fraps, Hooker and Forbes, 1949). The occurrence of progesterone in the non-laying female and in the male is not necessarily disturbing, for in the ovulating hen we are presumably dealing with periodic phenomena rather than with presumably steady states.

Circumstantial though the evidence for identifying the postulated excitation hormone as a progestin may be, this seems certainly a more likely possibility than that it is an oestrogen. The further investigation of periodic changes of both oestrogens and progestins in the blood stream of the ovulating hen will obviously be necessary to produce the definitive evidence, so notably lacking at present, as to the nature of the ovarian hormone controlling the hypophysial response (through whatever mechanism) expressed in OIH release.

NEURAL FACTORS IN FOLLICULAR MATURATION

Quite recently, it has been found that a number of agents believed to block the neural component of the OIH release mechanism may also suppress ovulation under conditions which apparently preclude direct suppression of the neural 'excitation' required for OIH release. As was stated earlier, phenobarbital sodium is highly effective in suppressing progesterone-induced ovulation, it has little or no effect

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when injected at 14 hours or at lesser intervals before expected C_1 ovulation, but it does block some 40–50 per cent of C_2 ovulations when injected at 9 hours before these are expected. These and other observations led us to ascertain the action of phenobarbital at increasing intervals before expected ovulation of C_1 and C_2 follicles in the usual 3-day cycle. The barbiturate was administered at 100 mg./kg. The hens were palpated at appropriate intervals during the day of, and at least one day following, expected normal ovulation. When phenobarbital injections resulted in interruption of normal feed and water intake, the birds were forcibly fed a mash carried in ample water.

The incidence of suppressed ovulations following phenobarbital injection at given hours is recorded in Table 15.23 (FRAPS and CONNER, unpublished). It is obvious that phenobarbital must be injected

TABLE 15.23
SUPPRESSION OF OVULATION BY PHENOBARBITAL SODIUM

Ovulation	To expected ovulation Hours	Hens injected, No.	Ovulations suppressed	
			No.	%
C_1	38	10	9	90
	34	11	9	82
	31	9	6	67
	27	7	6	86
	22	11	8	73
	18	12	3	25
	13	10	0	—
	9	10	0	—
			32	
C_2	23	11	11	100
	18	11	10	91
	17	14	12	86
	15	9	4	44
	13	12	6	50
	11	13	6	46
	9	12	5	42
	6	9	1	11
			44	

some 22 hours before C_1 ovulation, or about 17 hours before C_2 ovulation, to suppress any great proportion of expected ovulations. Unless we are prepared to accept an OIH release-ovulation interval even greater than that favoured by van Tienhoven *et al*, the results shown in Table 15.23 can scarcely be accounted to blockade of OIH release. Blockade of OIH release is also, certainly, most improbable as a

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consequence of phenobarbital injections 38 hours before C_1 ovulation. It seemed more likely that phenobarbital interrupted or suppressed processes of follicular maturation. In view of the well recognized selective action of phenobarbital sodium on the nervous system, it was thought, more specifically, that the barbiturate might act by suppressing, over neurohumoral pathways, the secretion of gonadotrophin required for follicular maturation.

To test this latter supposition, a number of barbiturates and 'blocking' agents were administered 38 hours before expected C_1 ovulation; the conditions of these experiments and results are given in Table 15.24 (FRAPS and CONNER, 1954). It is noteworthy that Dial and Nembutal, both of which tend to advance the hour of C_1 ovulation when injected 14 hours before the expected event, caused *only* suppression of C_1 ovulation when injected at 38 hours. The

TABLE 15.24

SUPPRESSION OF C_1 OVULATION BY BARBITURATES AND 'BLOCKING' AGENTS
ADMINISTERED AS A SINGLE INJECTION 38 HOURS BEFORE EXPECTED OVULATION

<i>Treatment</i>			<i>Hens injected, No.</i>	<i>Ovulations suppressed</i>	
<i>Agent</i>	<i>Route*</i>	<i>Quantity</i>		<i>No.</i>	<i>%</i>
Phenobarbital Na	Sc.	100 mg/kg	10	9	90
Dial	Im.	80 "	10	8	80
Nembutal	"	60 "	11	6	55
Dibenamine	Iv.	30 "	12	11	92
SKF-501	Im.	10 "	9	7	77
Atropine sulphate	Ip.	150 mg/hen	9	6	67

From Fraps and Conner (1954), by courtesy *Nature*, London.

* Sc., subcutaneous; Im., intramuscular; Iv., intravenous; Ip., intraperitoneal.

result following a single injection of atropine sulphate is of interest in view of the limited duration of action of this drug; the 67 per cent suppressed ovulations compares favourably with the 'blockade' of OIH (or LH) release reported by Zarrow and Bastian (1953) following 13 similar injections.

In a very large proportion (75-100 per cent) of hens in which ovulation failed to occur on the expected day, it also failed to occur on the day thereafter. The suppressed ovulations recorded in Tables 15.23 and 15.24 did not result, therefore, from a true blockade of OIH release. This conclusion is borne out by the prevalence of atretic follicles on the ovaries of hens autopsied within a few hours following time of normally expected ovulation (Fraps and Conner, unpublished).

These observations are believed to afford some evidence for the conclusion that the secretion of hypophysial hormones required for follicular maturation are controlled by a neurohumoral mechanism. It will be recalled in this connection that ROTHCCHILD and FRAPS

(1949b) found that the pituitary must remain intact for 2 to 4 hours following progesterone injection for ovulation to occur, indicating that the secretion of hormones required for maintenance of the follicle must continue for some time after OIH release. In the present experiments, we are apparently interrupting the same hypophysial secretions by 'blockade' of a neural component in the mechanism controlling the hypophysis, and independently of the presumably short term discharge of OIH (or LH) required for ovulation.

The dependence of follicular maturation in the hen on a neurohumoral mechanism, together with other considerations, led to the suggestion that the maturing ovarian follicle undergoes a process of pre-ovulating luteinization (Fraps and Conner, 1954). This possibility cannot be discussed at any length here, but if such preovulatory luteinization does occur, we have at hand a mechanism which meets at least the theoretical requirements for the production of progesterone (or a progestin) prior not only to ovulation, as occurs in the mammal (FORBES, 1953), but also prior to and as the condition for OIH release. In the closed cycle the preceding OIH release may of course serve also as the LH release for maturation (on preovulatory luteinization) of the succeeding—including the C_1 —follicle. Initiation of maturation processes in the first follicle of the isolated sequence, where there is no 'preceding' OIH release, presents us with a problem, the resolution of which may cast a good deal of light on the nature both of the excitation hormone and the neural component of the OIH release mechanism (see Fraps, 1954c).

Regardless of the mode of action of the 'blocking' agents listed in Table 15.24 on follicular maturation or maintenance, the fact that they do so introduces a question concerning the interpretation of results previously believed to indicate blockade of the OIH (or LH) release required specifically for ovulation. The apparent interval between excitation and ovulation may indeed be of the order indicated for the varying conditions of its determination discussed earlier. But in at least some instances these conditions may have involved interference with follicular processes rather than a true blockade of OIH release, or both effects may have been imposed. It is clear, in any event, that estimates of the interval between OIH release, or excitation for OIH release and ovulation must be made with caution pending a re-examination of the subject.

THE OVIDUCAL TERM AND THE MECHANISM OF OVIPOSITION

Warren and Scott (1935a) and Phillips and Warren (1937) observed that the ovum, following its ovulation, was engulfed by the mouth of the oviduct (the infundibulum) almost immediately. The time elapsing from ovulation of an ovum to its oviposition is therefore

practically identical with the time passed by the ovum in the oviduct, and may be referred to conveniently as the oviducal term. Since lay of the egg terminates the oviducal term, some of the factors which appear to be involved in the mechanism of oviposition are also considered here.

The Oviducal Term

The time required for the egg to traverse the oviduct varies at the same place from sequence to sequence, and at different places in the same sequence. The order of these differences is obviously of importance whenever variation in development of the ovum, or of the formed egg or its parts, is encountered at oviposition. Estimation of oviducal terms in general, if admittedly approximate terms, is accordingly desirable.

The oviducal term of the C_1 egg (O_1 to L_1 of *Figure 15.13*) is the time elapsing from O_1 to O_2 , minus the value of the interval between lay and associated ovulation. But the time elapsing from O_1 to O_2 is of the same order as the interval between the last two ovipositions of the sequence, and the value assigned to the interval between lay and associated ovulation was also assumed to be constant through the sequence. The oviducal terms of C_1 and C_n eggs are thus identical, and both are obtained directly as the interval between the last two eggs of the sequence minus the interval between lay and associated ovulation. This datum for the last egg is included in the general relation: the oviducal term of any egg (except the first) of a sequence is the interval between lay of the designated egg and lay of the preceding egg, minus the interval between lay and associated ovulation.

Intervals between successive ovipositions for our Beltsville Leghorns are given in Table 15.13, and intervals between lay and associated ovulation (i) in Table 15.5. Oviducal terms, calculated according to the relationship just stated, are recorded in Table 15.25. When $n = 2$, the single interval between successive eggs is 28.53 hours, and $i = 0.75$ hour. The oviducal term of the last egg (the C_2 in this sequence) is then $28.53 - 0.75 = 27.78$ hours. The oviducal term of the C_1 egg is the same. When $n = 3$, the interval between C_1 and C_2 eggs is seen to be 26.72 hours (Table 15.13) and $i = 0.61$ hour, whence the oviducal term of the second (C_2) egg is $26.72 - 0.61 = 26.11$ hours (Table 15.25). Similarly, the oviducal term of the C_3 egg is found to be 27.36 hours; this value is entered into Table 15.25 also as the term of the C_1 egg of the 3-member sequence. The same procedures are followed in estimating oviducal terms for members in the longer sequences.

The acceptability of these estimates of oviducal terms depends, like so many aspects of the cycle, on the degree to which procedures

used in estimating time of C_1 ovulation, and the interval between lay and associated ovulation (i) are valid. For reasons already discussed, then, the estimates shown in Table 15.25 are to be treated as approximations, formulating general relationships believed to exist in and between the oviducal terms in sequences of differing lengths rather than giving absolute values of oviducal terms.

In a paper on the relationship between shell thickness (and smoothness) and place of the egg in the sequence, Berg (1945) presented data which are of considerable interest in connection with the order of oviducal terms appearing in Table 15.25. In *Figure 15.21* (Berg's Figure 1), average shell thickness is shown at successive places

TABLE 15.25

ESTIMATED OVIDUCAL TERMS IN SEQUENCES OF WHITE LEGHORN HENS
(Beltsville)

n	i^* (hours)	Place of egg in the sequence					
		C_1	C_2	C_3	C_4	C_5	C_6
2	0.75	27.78	27.78	—	—	—	—
3	0.61	27.36	26.11	27.36	—	—	—
4	0.52	26.95	25.46	25.41	26.95	—	—
5	0.47	26.66	25.16	25.00	25.05	26.66	—
6	0.43	26.44	25.54	24.69	24.35	24.99	26.44

* i : the interval from lay to associated ovulation.

in sequences of 2 to 7 eggs. The shell of the second egg in the 2-egg sequence is seen to be thicker than that of the first. In sequences containing 3 or more eggs, the shells of the first and last eggs are thicker than are the shells of eggs in intervening positions. In sequences of 4 or more eggs, the shell of the first egg approaches or equals the thickness of the terminal egg.

Berg concluded that the shell of the last egg was thicker than that of eggs between first and last because of the longer time the terminal egg spends in the uterus. By the same reasoning, shell thickness at any place in a sequence should be at least roughly proportional to the time passed by the egg in the uterus (BURMESTER, SCOTT and CARD, 1939), and thus proportional to the oviducal term (Warren and Scott, 1935a, 1935b). Since oviducal terms of first and terminal eggs are estimated by our procedures to be equal (Table 15.25), these eggs should have (for the stated proportionality) shells of equal thickness. In sequences of 4 to 7 eggs, this equality is approximately realized (*Figure 15.21*). In the 2- and 3-egg sequences, the first egg has a thinner shell than the terminal egg, and one might then suppose the oviducal term of the first egg to be less than that of the terminal egg. However, the first egg is generally larger than

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other eggs of the sequence, and the same rate of shell formation by the uterus as a whole may result in a thinner shell over the larger egg. If this were so, the approximately equally thick shells of first and terminal eggs seen in the longer sequence ($n > 3$) would mean that the oviducal term of the first egg is actually somewhat greater than that of the last egg.

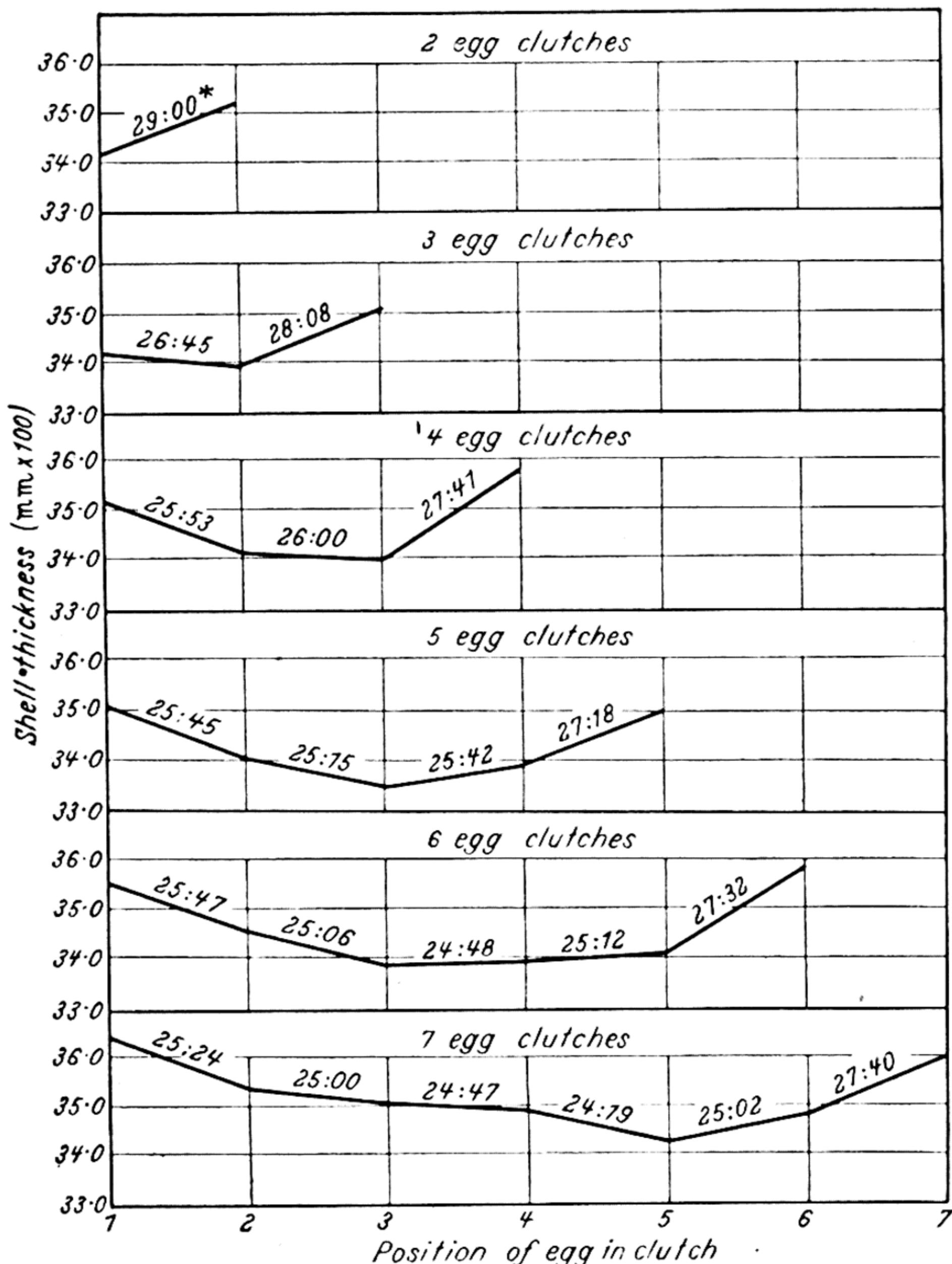


Figure 15.21. Average shell thickness and time interval between eggs, of eggs laid in different positions within sequences of different lengths. Figures on curves indicate average time interval between eggs. (From Berg (1945), by courtesy *Poult. Sci.*)

CONRAD and SCOTT (1942) noted that egg white accumulates in the magnum at a fairly constant rate during the interval between the passage of eggs, including the longer interval between passage of the terminal egg of one sequence and passage of the first egg of a succeeding sequence (one day lapse). These workers thought this might be a factor in the larger size of the first egg of a sequence. While

recognizing that the C_1 egg may have actually a longer oviducal term, Berg considered also that the uterus might function as does the magnum, the shell of the C_1 egg thus being thicker (when it is) than that of the succeeding egg because of the availability of greater quantities of shell forming materials. It is difficult to reconcile this view with the explanation for the thicker shell of the terminal egg, as was recognized by Berg.

It may be remarked that in sequences of 4, 5 and 6 eggs not only is the expected approximate equality of shell thickness in first and terminal eggs realized, but shell thickness of eggs in intervening positions (Figure 15.21) is in reasonably good agreement with the order of variation in oviducal terms approximated by our procedures.

As was noted earlier, fertilization of the ovum takes place very soon after ovulation, and the degree of embryonic development at oviposition should accordingly vary with the oviducal term. It is of some interest that TAYLOR and GUNNS (1935), McNally and Byerly (1936) and BERNIER, Taylor and Gunns (1951) have reported the first egg of the sequence to be slightly more advanced in development at oviposition than others of the sequence, including the terminal egg. While the evidence from embryonic development is not entirely consistent (see BERNIER, *et al.*, 1951), the oviducal term of the first egg would appear to be at least of the same order as that of the last.

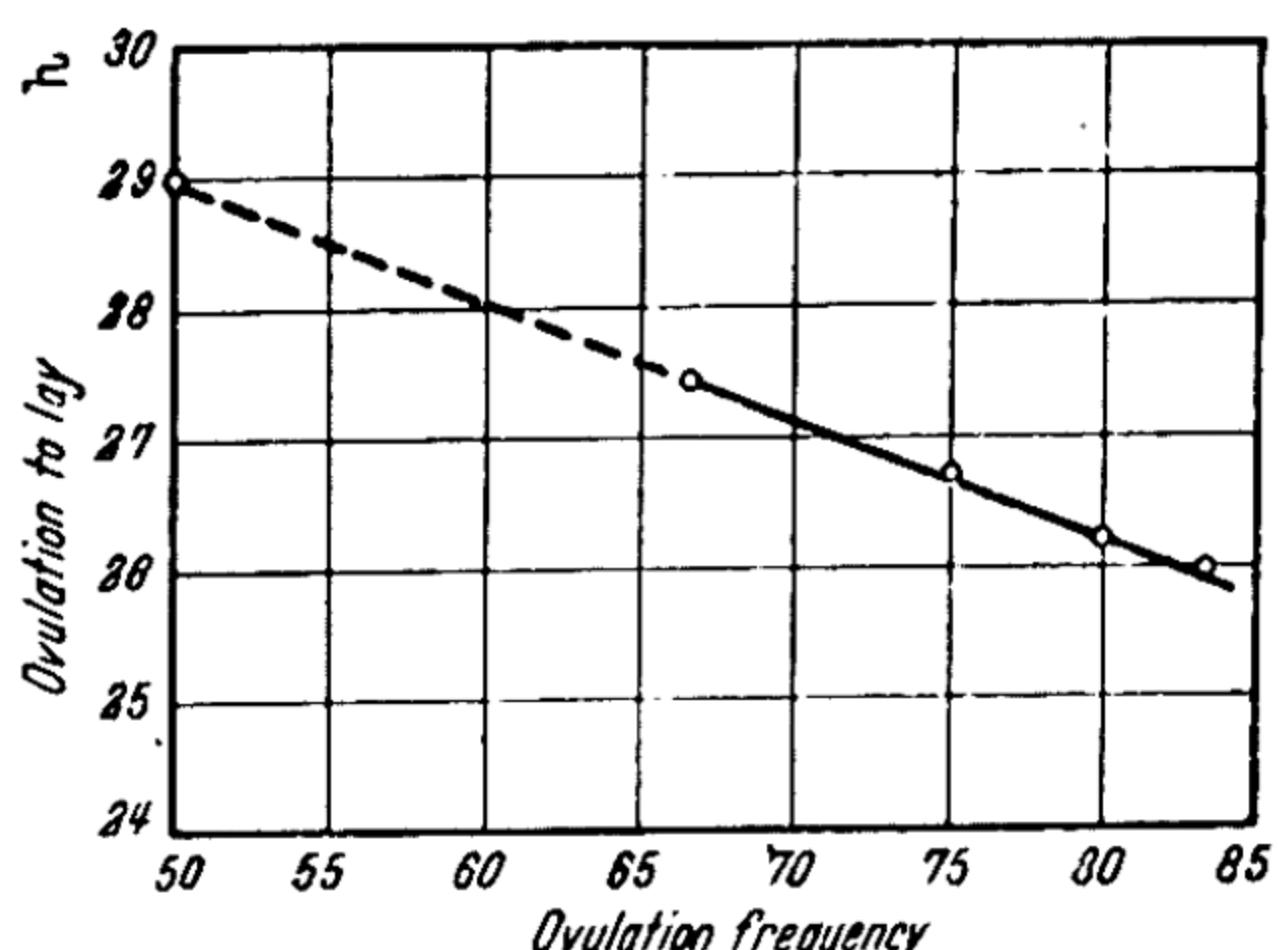


Figure 15.22. The oviducal terms of C_1 eggs as a function of ovulation frequency. Abscissas represent ovulation frequencies (f) calculated as $n/(n+1)$. The circles indicate hours from ovulation to lay of C_1 eggs in cycles for which $n=2$, 3, 4 and 5, corresponding to ovulation frequencies of 0.67, 0.75, 0.80 and 0.83. The oviducal term of the single egg in the 2-day cycle ($n=1$; $f=0.50$) is found, by extrapolation, to be close to 29 hours.

Further work on this problem, under rigorously controlled conditions, should prove rewarding.

The oviducal term of the single egg in the 2-day cycle ($n = 1$) is of course not included in estimates based on characteristics of the sequence. Rather limited observations (unpublished) indicate that the oviducal term of this egg is greater than any found in longer sequences. Ovulation of the single egg in the 2-day cycle occurs, on the average, later in the day than any other, and the mean time of its oviposition is also later than the C_1 egg of any other cycle (or sequence). All these characteristics are associated with the lower cycle frequency of the 2-day cycle ($f = 0.50$). In an attempt to express the oviducal term of the 2-day cycle as a function of oviducal terms of

first (or terminal) eggs of longer cycles, these latter were plotted against ovulation frequencies and the oviducal term of the single egg estimated by extrapolation (*Figure 15.22*). The value of about 29 hours is roughly of the order expected from palpation and autopsy data (Table 15.8). The relationships shown in *Figure 15.22* suggest, incidentally, that some other characteristics of the sequences might well be examined as functions of ovulation frequency.

The Ruptured and Ovulating Follicles in Oviposition

Despite interest in the possible homology of the ruptured ovarian follicle of the bird with the corpus luteum of the mammal (PEARL and BORING, 1918), nothing seems to have been known of any function in this ovarian element until Rothchild and Fraps (1944a) demonstrated that excision of the follicle resulted in failure of oviposition to occur at the normally expected hour. The ruptured follicle was removed at varying times following ovulation for effect on lay of the ovum it had previously contained. Results are shown in Table 15.26, together with results of other experimental procedures. It will be seen that excision of the most recently ruptured follicle (Group I) caused most hens (17 of 22) to retain their eggs for long after time of normally expected lay. Removal of the maturing follicle alone (Group II) delayed lay for a few hours in 2 hens, but when both the most recently ruptured and the maturing follicle were removed simultaneously (Group III) practically all hens retained their eggs beyond the hour of expected oviposition. Removal of the second ruptured follicle alone (Group IV) delayed oviposition in a small proportion of hens, and as in Group II, for a matter of a few hours rather than days.

Rothchild and Fraps noted that although the ruptured follicle appears to be the main factor in controlling lay of the ovum it previously contained, the ovulating follicle may also be a factor in timing oviposition. Evidence indicating that the ovulating follicle did in fact exhibit, to some extent, the properties of the ruptured follicle appeared in the observation that of the 31 hens holding their eggs (Group I and III, Table 15.26), 14 laid at the time of the first ovulation to occur following excision of the ruptured follicle. Further evidence appeared in the observation that if ovulation is forced to occur prematurely by only a few hours (3 to 6) before an expected oviposition, this oviposition also occurs prematurely by a few hours (FRAPS, 1942 and unpublished). Moreover, the usual relationship between lay and associated ovulation is maintained, oviposition occurring before ovulation, though both take place prematurely. It may be significant that if ovulation was forced by more than a few hours before an expected oviposition, the oviducal egg is not laid prematurely in association with the forced ovulation.

As has been noted in connection with Table 15.25, the oviducal term differs considerably from place to place in the same cycle. The capacity of the ovulating follicle to act, within limits, either alone or in concert with the ruptured follicle, affords a basis for understanding how these complex timing relationships may be realized. The timing of each oviposition except the last depends on the ovulating follicle, partially at least, and possibly altogether. Oviposition of the terminal egg occurs in the absence of associated ovulation; here timing of the event apparently rests entirely with the ruptured follicle. In the 2-day cycle ($n = 1$) all eggs are of course laid in absence of associated ovulation.

As we have seen in connection with Table 15.26, 14 of the 31 hens holding their eggs following removal of the ruptured follicle (Groups I and III, Table 15.26), laid in association with subsequent ovulation. The remaining 17 birds laid their retained eggs some time before, and independently of, ovulation. Some observation indicated that

TABLE 15.26

THE EFFECT OF REMOVING RUPTURED AND MATURING FOLLICLES ON RETENTION OF
THE EGG IN THE OVIDUCT AT TIME OF OPERATION

Group	Follicle removed	Age of oviducal egg, hr	Birds		Duration of delay in laying, range
			Operated on, No.	Retaining eggs, No.	
I	R ₁	0.5-26	22	17	9 hr to 3 days
II	M ₁	0.5-24	30	2	3 and 5 hr
III	R ₁ and M ₁	2.5-25	15	14	1 to 7 days
IV	R ₂	1.0-21	18	4	2 to 5 hr

R₁—The most recently ruptured follicle.

R₂—The second ruptured follicle in order of recency of origin.

M₁—The oldest maturing follicle, next due to ovulate.

From Rothchild and Fraps (1944a). By courtesy *Soc. Exp. Biol. Med.*

most of the retained eggs were laid during hours of light rather than in darkness. To examine the suggested relationship, the ruptured follicle and all pre-ovulatory follicles in the phase of rapid growth were removed from each of 48 hens (ROTHCHILD and FRAPS, 1944b). One group of hens (21) was continued under normal lighting conditions (lights 6 a.m.-8 p.m.), and another (27 hens) was placed under reversed lighting (lights 4 p.m.-6 a.m.). All except 4 hens retained their eggs. The remaining 44 hens were observed at appropriate intervals until the held eggs were laid. In each group the majority (17 hens in each group) laid their eggs during lighted hours, and in both groups oviposition occurred most frequently between 7

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and 10 hours following onset of light (Figure 15.23). It is of interest that 17 of 19 control hens similarly operated on, but with intact

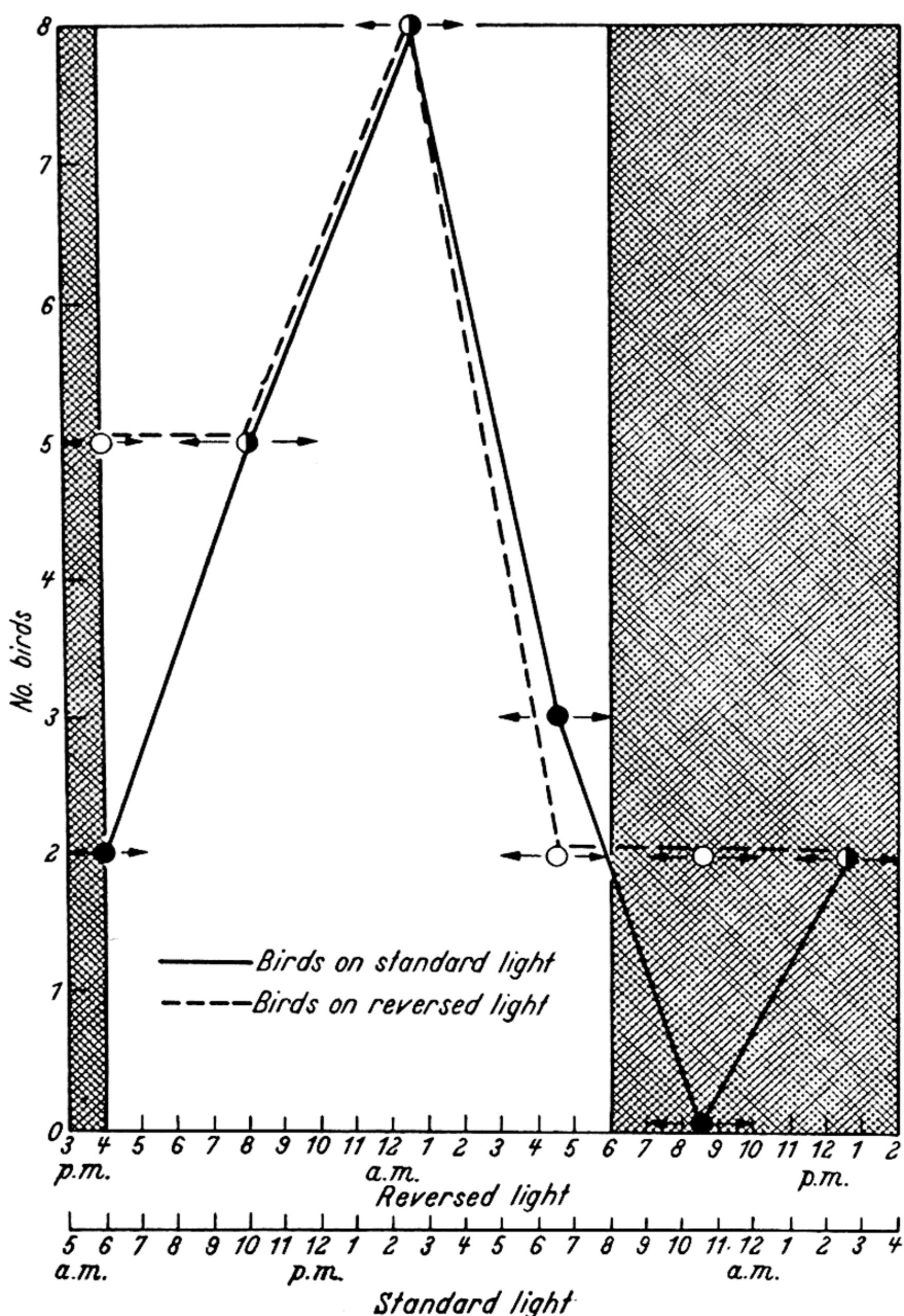


Figure 15.23. Lay of retained eggs by birds on standard and reversed light in relation to time of day. Only the hour of lay and the number of birds laying at the various hours are shown, irrespective of the length of retention. The shaded areas represent the dark portions of the day, the unshaded areas the light portions. The birds on standard light are represented by filled in circles and unbroken line, those on reversed light by the open circles and broken line. Where the values for both groups are the same a half filled in circle is used. (From Rothchild and Fraps (1944b), by courtesy *Endocrinology*.)

ruptured follicles, laid their eggs at approximately the normally expected hour, whether under standard lighting (6 birds) or under the reversed schedule (13 hens).

The association of oviposition with hours of light was not complete in hens lacking both ruptured and ovulating follicles, but it seemed of a sufficiently high order to justify the conclusion that some 'extra-ovarian, light sensitive agent is involved in the process of lay'. Rothchild and Fraps (1944b) speculated on the possibility that the agent in question was, or was associated with, the anterior pituitary gland. Subsequently, ROTHCHILD (1946) reported that removal of or injury to the anterior pituitary body did in fact delay oviposition in significant proportions of operated hens. Rothchild and Fraps (1944b) recognized also that the posterior pituitary body might be involved in the association of oviposition with light, since hormones from this lobe so readily induce oviposition in the dove (Riddle, 1921) and in the hen (BURROWS and BYERLY, 1942). Finally, there remains the possibility that the 'extra-ovarian, light sensitive agent' may reside in the central nervous system. If so, we might reasonably suppose the ovulating or the ruptured follicle to act through the same nervous apparatus in bringing about normal oviposition. It is tempting to think of the 'neural component' in such an hypothetical system as subject to diurnal periodicity in its sensitivity to ovarian or other stimuli, and as acting to cause the release of an 'oviposition-inducing' hormone from either the adenohypophysis or the neurohypophysis. While this view of the mechanism of oviposition is very largely speculative, there seems little doubt that nervous and endocrine factors are somehow intimately involved.*

In the pigeon, SCHOOLEY and RIDDLE (1944) found that variations in light (cloudiness, *etc.*) definitely affected time of oviposition, independently of any effect on time of ovulation. They thought it probable that posterior lobe hormone 'assists in the actual expulsion of the egg', but that there was normally a range of time over which reinforcement or 'triggering' of this action could be caused by the voluntary act of the bird. Schooley and Riddle noted other examples of 'psychic' control over oviposition in the pigeon, such as delay in lay of the second egg occasioned by failure of the incubating male to yield the nest (WHITMAN, 1919), or premature oviposition caused by rough handling or fright.

The participation of the nervous system in oviposition by the hen also seems fairly certain. WARREN (1930) noted that disturbing birds with eggs in their oviducts caused an appreciable increase in the interval preceding the next egg. SCOTT (1940) reported delayed oviposition to follow such relatively mild disturbances as handling of

* Since this was written, the author has learned from Prof. A. V. Nalbandov (personal communication) that hens from which the posterior lobe of the pituitary has been removed subsequently exhibit, upon recovery from the operation, substantially normal laying behaviour. While this observation would appear to rule out a role of the posterior pituitary lobe in oviposition, it is possibly significant that the posterior pituitary principles may be elaborated in the hypothalamus (Bargman and Scharrer, 1951), and are reported to occur in parts of the anterior pituitary body of the fowl (*vide infra*).

the bird or removing it to strange quarters, although ovulation was not prevented. Using the technique described by Huston and Nalbandov (1953), Sykes (1953a) noted that a loop in the uterus resulted in the premature lay of a large proportion of eggs, with little or no interference with ovulation. Presumably the effect is mediated, over neural pathways, to some more central mechanism which in turn causes oviposition, although this was not demonstrated.

WEISS and STURKIE (1952) showed that acetylcholine and histamine induce oviposition prematurely in the hen, an effect anticipated in view of the finding of MORASH and GIBBS (1929) and of MCKENNEY, ESSEX and MANN (1932), indicating that these substances contracted the uterus. The injection of ephedrine caused a delay in time of ovulation, in some hens for as much as 24 to 36 hours. Ovulation was apparently not affected, or at least not invariably, since malformed (second) eggs were occasionally laid after oviposition of the delayed egg. Weiss and Sturkie, on the basis of the available data, suggest that the hen's uterus is innervated by both cholinergic and adrenergic fibres, and that both 'are apparently involved in maintaining the normal tone of the tract'. They did not, however, suggest a direct role of these fibres in oviposition. It may be significant in this connection that SYKES (1953b) observed oviposition after spinal transection, although the process required longer than the usual time.

Weiss and Sturkie (1952) also noted that soft and imperfectly shelled eggs are frequently laid by hens with or recovering from Newcastle disease, and that this disease frequently involves the nervous system. GRAU and KAMEI (1949) made the interesting observation that delayed oviposition occurred among hens fed purified diets, but the locus of failure was not ascertained.

The obvious problem presented by these observations is to determine whether the nervous factors leading to premature or delayed oviposition act directly or, as has been suggested, through the release of a hormone which in turn causes oviposition.

Oviposition in the hen usually occurs within 3 to 5 minutes following injection of pituitary lobe extracts, and in this species the pressor as well as the oxytocic principle is effective (BURROWS and FRAPS, 1942). The response to the pressor fraction is fairly uniform from the time the uterine egg is completely plumped, and removal of the ruptured follicle soon after ovulation did not alter the response to injections made a few hours before expected oviposition (ROTHCHILD and FRAPS, 1946). Morash and Gibbs (1929) showed that pituitrin caused uterine contractions, and contraction in uterine strips *in vitro* was demonstrated by MCKENNEY, ESSEX and MANN (1932). It is to be noted that all of the posterior lobe principles are found in the posterior pituitary lobe of the chicken, and in small quantities in

parts of the anterior pituitary body (DELAWDER, TARR and GEILING, 1934).

The dependence of terminal oviposition in the cycle solely upon the ruptured follicle has been advanced as the explanation of the longer interval between the last two ovipositions (ROTHCHILD and FRAPS, 1944a). According to the estimates appearing in Table 15.25, however, the oviducal terms of the first and terminal eggs are identical, which means that the 'age' of the ruptured follicle is of the same order at oviposition of C_1 and C_n eggs. Occasionally, at least, the oviducal term of the C_1 egg would appear to be even greater than that of the C_n egg, and it might be supposed that oviposition of the C_1 egg was effected by the ruptured rather than by the ovulating follicle. If, however, the C_2 ovulation is suppressed, as with oestrogen, the C_1 egg is usually laid later in the day than when laid in association with C_2 ovulation. There is at least a suggestion here that the ruptured follicle may act through an intermediary mechanism which is subject to diurnal periodicity in its thresholds of response to a hormone produced by the ruptured follicle. The possible role of the nervous system (the hypothalamus?) in this capacity has already been noted.

Mention should be made of one last item regarding the ruptured follicle. Excision of the entire structure causes delay in ovulation, as has been noted. Removal of about half of the ruptured follicle results, however, in premature lay by a substantial percentage of hens (Conner and Fraps, 1954). The significance of this effect is not known, but it clearly underscores the need for identification of the hormone, or hormones, secreted by the ruptured follicle.

FERTILITY PROBLEMS IN POULTRY

The problem of infertility may not be more serious in poultry than in other farm animals but because of the manner of reproduction, it is much more apparent. The wastage of human food from the settings of infertile eggs is tremendous and the financial loss due to infertility in turkeys and chickens raises the cost of poultry meat considerably.

The gravity of the situation is pointed up in a report from the Oregon Agricultural Experiment Station (MUMFORD, 1952). In this study records from 77 flocks totalling more than 58,000 turkey hens were analysed. The average seasonal hatch was 60.4 per cent of all eggs set. This low figure represents both lack of fertility and hatchability with the former probably the more important. The situation is somewhat less serious with chickens, as the national (U.S.A.) average hatch of all eggs set is estimated to be 65 to 70 per cent with about 15 per cent of the eggs being infertile. The important

research to the date of publication has been adequately reviewed by Landauer (1951), Taylor (1949) and Sturkie (1954). A further review of this material at this time seems unnecessary.

Until quite recent years, biologists have thought fertility, at least within the higher order of animals, was an 'all or none phenomenon', and that all fertilized eggs had more or less an equal chance of normal development in so far as the condition of their fertilization was concerned. There is a growing amount of evidence indicating that this general thought must be revised. This is well exemplified in the report of Nalbandov and Card (1943), who studied the effect of the natural aging of spermatozoa in the oviduct on hatchability. They found that with increasing age of sperm, there was an increasing proportion of fertile eggs which failed to hatch. Also, that the age of the embryo at death was a sensitive indicator of the age of the sperm. Dead embryos from eggs fertilized by fresh sperm died, on the average, on the 14th day of incubation, while eggs fertilized by sperm that had been in the oviduct from one to ten days, died at about 11 days of embryonic development. Eggs fertilized by sperm older than 11 days died, on the average, at one to five days of development.

Further evidence giving impetus to this concept is found in reports by OLSEN (1941, 1942). Olsen studied the normal changes in the blastodiscs of hens' eggs just previous to and following ovulation. He found that the egg is normally fertilized in the infundibulum within 15 minutes of ovulation, and he confirmed the previous observation that 3 or 4 sperm cells normally enter the egg at the time of fertilization. He found that the second polar body was extruded following the penetration of the sperm before and simultaneously with the fusion of the male and female pronuclei. The first segregation division occurs about five hours after ovulation, and the 4th and 8th cell cleavage stages are arrived at while the egg is still in the isthmus of the oviduct. Olsen studied the fate of the unfertilized egg and found that fragmentation processes sub-divided the protoplasm in the infertile egg in much the same manner as does the true cleavage of the fertile egg. Once this fragmentation process has begun, the blastodiscs are incapable of resuming development even though stimulated by sperm cells.

Considerable variation has long been noted in the developmental stage of the egg at the time of laying, and it has been thought that the extent of development had in turn some bearing on the hatching potential of the egg. The degree of development naturally would be expected to be associated with the oviducal term, which has been shown to vary considerably with place in sequences of varying length, and with holding temperatures. SCOTT and WARREN (1936) and McNally and Byerly (1936) found considerable variation among chicken embryos after the eggs had been incubated for a short period

of time. In both of these studies the number of somites in an embryo following a definite number of hours of incubation served as an index for estimating the degree of development, and the greater number of somites was associated with a higher percentage of hatch. In other words, the more rapidly the embryo begins to grow and develop, the better the chance that it will complete the process. This same general phenomenon has been observed in turkey eggs by OLSEN and MARSDEN (1950), who found that it was possible to segregate turkey eggs of high hatchability from those of low hatchability by candling after only 18 or 24 hours of incubation.

These reports led some investigators to feel that some eggs, while appearing to have a certain degree of embryonic growth, were incapable of completing normal development. GOWE (1950), for example, discussed the appearance of 'degenerate' chicken egg blastoderms which he thought incapable of normal development. KOSIN (1951) described in detail the appearance of turkey embryos in various states of morbidity. Still further light has been brought to bear on the situation with the disclosure by Olsen (1942) and KOSIN (1945), that there are nucleated cells in unfertilized chicken eggs. These authors came to the conclusion that some abortive type of parthenogenesis does occur in the eggs of some chickens. Further evidence that parthenogenesis, at least in the turkey, is a rather common occurrence, has been reported by OLSEN and MARSDEN (1954a, b). An account of the phenomenon of parthenogenesis in the turkey egg appears elsewhere in this text.

In summary then, it seems that at least three types of embryonic development are possible. First, the egg may be fertilized by a normal vigorous sperm cell at the opportune time and normal development will result. Second, a normal egg may be fertilized by a sperm of low vitality which may initiate embryonic development, but development does not go to completion. And third, there may be a type of parthenogenetic development which, in most cases, does not result in complete embryonic development. It would appear that the most logical approach for improving the reproductive performance of birds would be to select them on the basis of the number of poult or chicks hatched in relation to the total number of eggs set. In other words, the phenomena of fertility and hatchability are very closely associated and interdependent and any plan for improvement must include both phenomena.

Apparently, little doubt remains that fertility is an inherited character. GOWE and HUTT (1949) studied fertility among three strains of White Leghorns and concluded that since no new blood had been introduced into these strains for 14 years and since there were consistent differences in fertility, that the infertility observed was of genetic origin. HAYS (1949) observed the fertility within

Rhode Island Red families over a period of 10 years and concluded that fertility is partly controlled by genetic factors and that there was some evidence that sex-linked genes were involved.

HARPER and PARKER (1950) followed the fertility of broad-breasted turkey hens inseminated at bi-weekly and longer intervals and concluded that there were family differences in the fertility of the hens irrespective of the type of insemination programme. WHITSON, MARSDEN and TITUS (1944) studied the fertility and hatchability of standard bred Bronze, White Holland, Broad Breasted Bronze and Beltsville Small White turkeys. These authors concluded that the Broad Breasted Bronze turkey had significantly lower fertility of all eggs laid than the other varieties. WALTER and HOFFMAN (1947) also found that there were differences in the degree of fertility between different varieties of turkeys.

A more definitive study of the inheritance of fertility in turkeys was carried out by BLOW, *et al* (1951), who analysed data on the fertility of 73 pairs of sisters, each of which were mated to the same male. This study indicated that fertility is influenced by heritability and that the heritability of fertility is of a relatively low order. In other words, the environmental influences were likewise relatively important in determining the performance of various individuals with respect to fertility. Nevertheless they concluded that considerable progress can be made where it is possible to select for high fertility.

A study of the factors affecting fertility in the turkey was undertaken by SMYTH and LAIGHTON (1953), who concluded that the hen is responsible for initiating matings whereas the successful completion of matings is dependent upon the male. The incidence of broodiness, number of eggs laid and environmental temperature did not appear to exert an influence on the fertility and therefore much of the apparent infertility appeared to be explained by the low mating frequency on the part of the female or inefficiency on the part of the male. They found statistically significant differences in ability to mate successfully among the seven males used.

The above observations leave little doubt that fertility within any given population is influenced by heritability and that considerable improvement could be expected if birds were vigorously selected for this character. Such a selection programme should take into account the overall hatch from all eggs set; and since the male and female both contribute to the outcome, selection should be applied to both sexes.

It should be noted, however, that factors other than those of genetic origin may cause infertility and poor hatchability. For example, unfavourable environmental conditions that give rise to frozen combs or wattles, colds, or moult are factors affecting fertility adversely. In recent studies OLSEN and MARSDEN (1952) have shown

that in turkeys, moult on the part of the tom is closely associated with the seasonal drop in fertility. These workers found also that too much light, either as too long a light day or of too great an intensity, caused the males but not the females to moult.

PARTHENOGENESIS IN THE AVIAN EGG

It has long been known that some of the eggs of certain insects such as bees and aphids can develop without having been fertilized. This type of development, known as parthenogenesis, also can be induced artificially in the eggs of some invertebrates. Until recently, however, it was still a debatable question as to whether parthenogenesis can and does occur in the eggs of birds.

Discussion as to whether parthenogenetic development was possible in the case of birds began as early as 1872 when OELLACHER reported finding cell-like bodies in sections of the germinal discs of infertile chicken eggs, some of which he found to be nucleated. This finding was later confirmed by DUVAL (1884) and by LECAILLON (1910). On the other hand, LAU (1894), BARFURTH (1896) and LILLIE (1919), although finding the cell-like structures, came to the conclusion that they were not true cells since they were unable to find nuclei. They were of the opinion that these objects resembling cells were formed as a result of fragmentation of the disintegrating disc.

The subject of parthenogenesis in bird's eggs did not again receive serious attention until 1924 when BARTELMEZ and RIDDLE reported finding nucleated cells in the infertile germinal discs of newly laid pigeon's eggs. This was followed with studies by HAYS and NICOLAIDES (1934), Olsen (1942) and KOSIN (1945, 1948), each investigator using for experimental material newly laid, infertile eggs. Olsen (1942) and Kosin (1945) reported finding nucleated cells in unfertilized chicken eggs and came to the conclusion that an abortive type of parthenogenesis does occur in the eggs of some chickens. Hays and Nicolaides (1934), finding no nucleated cells in the discs of newly laid Rhode Island Red eggs, came to the conclusion that parthenogenesis does not occur in the case of the chicken egg. Kosin, in his study of 100 blastodiscs, was able by application of the Feulgen test to demonstrate chromatin in the nuclei of certain cells and concluded that parthenogenetic cells were present in 15 per cent of the blastodiscs. His findings led him to conclude that an abortive type of parthenogenesis does occur in the egg of the domestic chicken, that the process is of short duration and that these cells could not be revived by incubation.

Good evidence that parthenogenesis is of natural and of quite frequent occurrence in unfertilized eggs of some species of birds has been reported recently by OLSEN and MARSDEN (1953, 1954a, b).

EGG PRODUCTION AND FERTILITY IN POULTRY

The history of their early observations is of some interest. Beltsville Small White turkeys were under test in studies to ascertain the causes of a premature moult of male birds, and to determine whether the seasonal decline of fertility of turkey hatching eggs was or was not correlated with the loss of feathers by the males. To accomplish this second objective, a tester flock of 29 unmated Beltsville Small White females was maintained. These females had been isolated from males for 56 days at the time they were to be used in testing, but in view of the long survival of turkey spermatozoa within the body of the female, it was decided to test some of their eggs for fertility before mating the birds. With this thought in mind, eggs from these 29 females were placed in an incubator for 7 days before examining them for fertility. This is a routine practice at Beltsville, since after 7 days of incubation embryonic growth, if present, can be detected with ease either by candling or on breaking the eggs. Thus, these studies, unlike those of former investigators, were based on observations made after the presumably infertile eggs had been incubated for a period of 7 days or longer.

On breaking these eggs, a retarded type of cellular growth was encountered. Repeated tests at weekly intervals thereafter showed the same type of growth in eggs laid as long as 200 days after there was any chance of mating. For the most part, this growth was abnormal in so far as it required at least three days of incubation before there was any discernible change in the macroscopic appearance and size of the germinal disc. Furthermore, in the majority of instances (98 per cent) only the extra-embryonic membranes were present, no embryo having been formed. In spite of the fact that no embryo was present the cells in most instances continued to multiply until the membranes had covered most of the surface of the yolk. On the average, 16.7 per cent of the eggs from these 29 non-mated turkeys after the 7-day incubation period showed development of this type. These results are described by Olsen and Marsden (1953, 1954a).

The typical three- or four-day delay in development has been encountered also in some eggs from mated turkey hens, suggesting that parthenogenesis may occur in unfertilized eggs from hens of mated flocks (Olsen and Marsden, 1954c).

During 1954, 79 virgin Beltsville Small White turkey hens were tested by Olsen and Marsden. During an 8-week period (March 6-May 10), special measures were taken to insure against mistaken identity of the eggs. During the 8-week period, a total of 2,537 eggs were laid by the 79 hens. Of this number, 568 or 22.4 per cent showed parthenogenetic development. In 492 of these 568 eggs, the development consisted solely of growth of the extra-embryonic membranes. In 49 of the 568 eggs, differentiation proceeded to the extent that blood islands or blood vessels were clearly visible by candling and

on macroscopic examination. In the remaining 27 of the 568 eggs, embryos were identifiable on gross examination. These embryos attained to various stages of development, and are listed below in terms of equivalent development of the normal turkey embryo (from OLSEN and MARSDEN, 1954b):

2-3 days	8 embryos
4-5 days	11 embryos
9-10 days	3 embryos
14-18 days	2 embryos
26-27 days	3 embryos

Chromosome counts were made of parthenogenetic cells by YAO and OLSEN (1955). These workers found the cells to contain the diploid number.

From these results we must conclude that not only does natural parthenogenesis occur but that it is possible in some cases for an embryo to be formed and to go almost to completion of the incubation period. Parthenogenetic development has also been observed in two other varieties of turkeys, Broad Breasted Bronze and Light Palms. In the case of both these varieties approximately 11.5 per cent of all eggs laid show this type of development.

Unfertilized eggs of certain breeds of chicken have likewise been tested by incubating them for 7 days. These included Rhode Island Reds, New Hampshire, Dark Cornish and Dark Cornish crosses. Only the Dark Cornish breed had an appreciable number of eggs with parthenogenetic development, some 13.5 per cent of all eggs set. The Dark Cornish crosses showed 1.5 per cent, while eggs of the two other breeds failed to exhibit a single instance of development of this type (OLSEN and MARSDEN, 1954d). These results with chicken eggs are of interest since the work of Kosin and others have shown that parthenogenetic cells are formed in the discs of eggs of our more common domestic breeds while the egg is in the oviduct of the fowl. It would seem that the parthenogenetic cells in the eggs of some breeds of chickens differ in their ability to remain alive and revive upon incubation.

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